

CARBONIFEROUS ORTHOSTERNI AND THEIR RELATIONSHIP TO LIVING SCORPIONS

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ABSTRACT. Five species of Upper Carboniferous orthostern scorpions are described from Britain and North America. Two are established taxa, and three are new: *Palaeopisthacanthus vogelandurdeni* sp. nov., *Cryptoscorpion americanus* gen. et sp. nov., and *Corniops mapesii* gen. et sp. nov. An additional species, *Gymnoscopus mutillidigitus* gen. et sp. nov., is referred to the suborder Neoscorpionina, but is too incompletely known for its systematic position to be determined more accurately. The descriptions are based on fragmentary material from dispersed arthropod cuticle assemblages. These have yielded sufficient anatomical detail to assess the relationship between fossil and Recent orthostern scorpions for the first time. A cladogram is presented, demonstrating that Carboniferous orthosterns comprise the stem group from which all Recent scorpions (the crown group) were derived. The recognition of important character state transition series in the Orthosterni, and their polarities, will facilitate more accurate assessment of the relationships between modern scorpion genera.

THE fossil record of scorpions has been largely ignored by neontologists in discussions about the origins of modern scorpion families and the relationships between them. This is understandable, as the quantity of fossil data having a bearing on these problems is small, and its quality poor. Most fossil scorpions are Palaeozoic forms, and the handful of described Mesozoic species are essentially Palaeozoic relics. By contrast, all reasonably well preserved Cenozoic fossil scorpions are thoroughly modern in aspect and can be assigned to extant families, if not genera (e.g. Schawaller 1979, 1981).

Among fossil families, only the Palaeopisthacanthidae span the gulf between the diverse Palaeozoic record of scorpions and the Cenozoic to Recent fauna. Kjellesvig-Waering (1986) included two Upper Carboniferous species in this family, *Palaeopisthacanthus schucherti* Petrunkevitch, 1913, and *Compsoscorpionus elegans* Petrunkevitch, 1949. One specimen of the former species, and three of the latter, were available to Kjellesvig-Waering. These are reasonably well preserved in ironstone nodules, but even so, most anatomical details which are of importance in the classification of Recent scorpions cannot be ascertained, and Stockwell (1989) concluded that these species are so 'modern' in their gross morphology that if more characters were available, they could probably be placed within Recent superfamilies.

A systematic search for dispersed scorpion cuticle fragments in Carboniferous sediments has yielded exceptionally well preserved material which reveals morphological detail unobtainable from typical scorpion body-fossils (Bartram *et al.* 1987). During the course of this study in excess of 20000 cuticles (a conservative estimate) from twenty two Carboniferous localities have been examined. The material is largely fragmentary, consisting of cuticle scraps (around 80% of most assemblages), isolated exoskeletal elements, and very rarely, associated body parts from a single individual. Palaeopisthacanthid cuticle forms only a small proportion of each scorpion cuticle assemblage, but even tiny fragments are easily recognizable because they have a distinctive surface ornament. This paper describes all of the palaeopisthacanthid material recovered to date, and two additional forms which have closer affinities to the palaeopisthacanthids than to any other Carboniferous family.

LOCALITIES AND MATERIAL

Localities

Details of localities from which the palaeopisthacanthid type of cuticle has been obtained are listed below in stratigraphical order. The productive lithologies are either coals or carbonaceous shales rich in comminuted plant debris, and all appear to have been deposited in forested flood-basin environments.

1. Goyt's Clough, near Buxton, Derbyshire, England; NGR SK 0272. Shaly coal from the top 0.3 m of Goyt's Coal; basal Westphalian A.
2. Glodwick Brickworks, Oldham, Lancashire, England; NGR SD 9404. Bituminous coal from the Blenfire Seam; high Westphalian A.
3. Coby Carr Quarry, near Todhills, Co. Durham, England. Bituminous coal from the Bottom Busty Seam; high Westphalian A.
4. Pemberton Opencast Mine, Near Wigan, Lancashire, England. Carbonaceous shale from a seam split in the Wigan Five Foot Coal; uppermost Westphalian A.
5. Swillington Brickpit, Swillington, Yorkshire, England; NGR SE 385315. Carbonaceous shales occurring as seam splits and roof shales in sequences of thin coals at three horizons (beds 13, 18, and 20F of Scott (1978, 1984)); low Westphalian B.
- 6a. Lowther North Opencast Mine, near Leeds, Yorkshire, England; NGR SE 403282. Bituminous coal from the Barnsley Seam; low Westphalian B.
- 6b. Wistow Mine, Yorkshire, England; NGR SE 5936. Bituminous coal from the Barnsley Seam; low Westphalian B.
7. United Electric Companies Banner Mine, Foulton County, Illinois, USA; SE1/4, NW1/4, Sec. 12, T. 6N, R. R. 5E. Bituminous coal from the Colchester (no. 2) Coal, Carbondale Formation; Westphalian D (Desmoinesian).
8. Lone Star Lake Spillway, Douglas County, Kansas, USA; NW 1/4, Sec. 13, T. 14S., R. 18E. Carbonaceous shale from immediately above the Lower Williamsburg Coal, Douglas Shale Formation; Stephanian B (Virgilian). See Landingham (1961) for further details of the locality.

Material

All cuticle material used in this study is deposited at the Ulster Museum, Belfast (BELUM). For brevity the Ulster Museum code (BELUM) has been omitted when referring to cuticle specimens in the text or figure legends, which are all prefixed by 'K'. Body fossils referred to in the text are located at the Natural History Museum, London (BMNH), and Yale Peabody Museum (YPM). The Appendix lists all significant cuticle specimens used in this study, but unidentifiable sclerites and cuticle scraps derived from palaeopisthacanthids are not listed.

METHODS

Standard palaeobotanical techniques were employed for the extraction of dispersed arthropod cuticles from sediment bulk samples (e.g. Funkhouser and Evitt 1959; Staplin *et al.* 1960). Coals were macerated in fuming nitric acid, but exposure to acid for more than two to three hours resulted in some corrosion of scorpion cuticles, and exposure for over one day destroyed them. It is possible that this treatment removes cuticles of some arthropod groups which are less acid resistant, but there was no way to check this. Dark carbon-rich shales were disaggregated efficiently in 100 volume hydrogen peroxide, whilst soft shales were soaked in dilute potassium hydroxide solution for several days.

Residues were wet sieved, and typically consist of a mass of plant cuticles, palynomorphs, carbonized plant material and occasional arthropod cuticles. The smallest useful fraction was retained on a 250 μm aperture sieve. Finer residue fractions were routinely checked for the presence of microarthropod remains. Residues were examined under water by transmitted light, which enables arthropod cuticles to be picked readily from among plant debris. Cuticles were stored in two percent hydrochloric acid, since those stored in water are readily susceptible to fungal and bacterial attack.

Before mounting on microscope slides, material from shales generally required cleaning to remove adherent clay minerals which obscure detail in transmitted light. Most clay can be removed mechanically with a fine needle, but the best results were obtained by soaking batches of cuticle in sixty percent hydrofluoric acid for

several hours. Organic material, much of it opaque, is often so firmly bonded to the cuticle that it is difficult to remove without damaging the specimen.

Many specimens were folded on themselves prior to burial (see below), but in some cases these can be unfolded by careful manipulation in the mounting medium before the cover slip is positioned. The study of flattened cylindrical sclerites, such as postabdominal segments, is facilitated by slitting the cuticle along one margin. The opposed layers of cuticle can then be separated and mounted as a single sheet rather than two surfaces compressed together.

Specimens were mounted on glass microscope slides in glycerol jelly, Aquamount, or Aqualite. Transmitted light microscopy proved to be the most useful means of study, employing an Olympus SZH Stereo Zoom Microscope, and a Nikon Optiphot biological microscope fitted with a Normaski Differential Interference Contrast (NDIC) facility.

Specimens are oriented in the illustrations with anterior ends towards the page top, with the exception of prosomal appendage sclerites, which are oriented with the superior surface towards the page top and distal end to the right, unless otherwise indicated in the legend. Explanatory figures were prepared from *camera lucida* drawings made on the Olympus SZH microscope. Stippled areas are internal cuticle surfaces and dotted lines represent linear features showing through the cuticle from behind. In specimens with overlapping layers of cuticle, e.g. podomeres, cuticular features such as follicles, spines and tubercles on all layers are shown, not only the uppermost. Artifacts, plant debris and opaque organic matter have been omitted from most text-figures. Abbreviations used in text-figures are as follows: St, sternite; T, tergite; Co, coxa; Ca, coxal apophysis; S, sternum; Cp, carapace; Go, genital opercula; tf, anterior transverse ridge; sm, stigma; ic, inferior carina; sc, superior carina; im, inferior median carina; il, inferior lateral carina; sl, superior lateral carina; dc, dorsal carina; ss, secondary tubercular structure; b, basal tooth; m, median tooth; sd, subdistal tooth; d, distal tooth; i, inferior row of teeth; a, ?arachnid podomeres; mi, mite remains; ts, tibial spur; dt, dorsal tubercle; le, lateral eye node; me, median eye; fe, femur; tr, trochanter; D, opaque detritus.

Trichobothrial terminology and abbreviations used are those of Vachon (1973), whilst podomere terminology follows that of Couzijn (1977), and other scorpion terms are those recommended by Stahnke (1970).

PRESERVATION AND TAPHONOMY

Preservation

The material is preserved as thin sheets of organic cuticle (Bartram *et al.* 1987). The sheets are flexible when wet, but become brittle on drying. Average cuticle thickness is 2–4 μm , the thinnest cuticles being almost colourless, with thicker ones (from larger individuals) grading from pale yellow through to orange-brown. Most specimens recovered are small scraps of cuticle consisting of a single sheet. Fragmentary material which can be recognized as a particular sclerite type is scarce, and complete sclerites or associated groups of sclerites (i.e. partial individuals) are rare. All material is compressed, leading to complex collapse folding of the originally three dimensional structures. In other respects the cuticle preservation is similar to that described by Selden *et al.* (1987) for Devonian arachnid cuticle compressions. Scanning electron microscopy (SEM) of thick cuticles from very large Carboniferous (non-orthostern) scorpions has revealed that only an outer region of the cuticle equivalent to the hyaline exocuticle of Recent scorpions is preserved. The thinness of preserved cuticle, in relation to the original body length of these scorpions, suggests that this is also the case for the orthostern cuticle described below.

Taphonomy

Dispersed scorpion cuticles are invariably preserved in association with fragmentary plant cuticles and palynomorphs. They are most frequently encountered in horizons rich in comminuted plant debris, such as the roof shales of coal seams and shaly partings (splits) within seams. The great majority of cuticles are derived from immature individuals, but occasional larger specimens indicate the minimum adult sizes reached by each taxon. The cuticle could be derived from moulted exoskeletons or dead animals. There is little direct evidence for the latter, apart from some rare

aggregates of finely comminuted cuticle which may be arachnid rejectamenta, or possibly the remains of cuticle rich coprolites. Evidence for moulted integuments is more frequent, and includes 'telescoped' abdominal regions, and distal podomeres which were pulled inside proximal ones as the leg was extricated from the exuvium.

Maceration residues contain a range of material with different degrees of fragmentation, which on the basis of sclerite sizes must have come from many different individuals. Most disarticulation and comminution, therefore, occurred prior to burial, although the occurrence in a residue of fragments which can be fitted together suggests that some fragmentation of sclerites, but not individuals, was due to diagenetic compaction of the cuticle and/or the cuticle recovery process.

A variable proportion of cuticles in each assemblage show evidence of partial degradation by saprotrophic microorganisms. Corrosion of the outermost preserved layer of cuticle is common, and SEM examination of corroded surfaces reveals clusters of small pits which may be attributable to the former presence of bacterial plaques. More convincing evidence is provided by star-shaped scars with anastomosing branches, identical to those attributed to actinomycetes in palynomorphs (Elsik 1971). No remains of the saprotrophs responsible were found *in situ*, ruling out the possibility that the degradation is due to recent contamination.

A few cylindrical sclerites contain the remains of mites, or other arthropods, compressed between the two layers of cuticle. Mites may have entered the disarticulated sclerites to feed, or perhaps used them as moulting refugia, but in either case owe their preservation to this habit since, with the exception of the Lone Star Lake assemblage, articulated mite remains do not occur free in the cuticle assemblages examined.

The cuticle assemblages probably represent detrital arthropod material accumulated in a leaf litter layer. Residence times of cuticle in the litter were variable as evidenced by the different degrees of comminution and degradation shown by cuticles in an assemblage. Rapid establishment of post-burial anoxic conditions may have been a prerequisite for preservation because scorpion cuticle, including the hyaline exocuticle, is rapidly degraded in aerobic conditions (pers. obs.; but see Allison and Briggs 1991 on the role of anoxia on soft-bodied fossil preservation). Since non-hyaline procuticle (inner exocuticle and endocuticle) is not present in the fossil material, the decomposition of these layers probably continued after burial in an anoxic environment. An abundance of plant material buried in association with the scorpions may have been a significant factor in the reduction of available oxygen in the sediment. Why anaerobic saprotrophs did not continue degrading the scorpion cuticle (and indeed the plant cuticle) after burial is unknown.

No remains of uniramians were found in any assemblage, and cuticle of other arachnids only occurred in assemblages where scorpion cuticles display very low average degrees of degradation. The scorpion hyaline exocuticle layer is apparently unique to scorpions (Hjelle 1990), but an analogous layer may also occur in xiphosurans and eurypterids (Dalingwater 1986). Scorpion hyaline exocuticle (or its equivalent in Palaeozoic scorpions) appears to be far more resistant to anaerobic decay than the cuticle of other arthropods.

DISPERSED CUTICLE TAXONOMY

The difficulties involved in dispersed cuticle taxonomy were discussed by Wills (1947). His work on a Triassic cuticle assemblage is the only previous study which has attempted to deal with dispersed material, and his methods are adopted here, with some modifications. More recently, a Middle Devonian arthropod cuticle assemblage, the Gilboa fauna, has underlined the value of such material, radically altering our perception of early terrestrial faunas (Shear 1990). However, until now, taxonomic work on the Gilboa fauna has relied heavily on the rare occurrence in that assemblage of relatively complete specimens to which the more fragmentary remains add supplementary data (Shear *et al.* 1987; Selden *et al.* 1991).

The Upper Carboniferous assemblages from which the palaeopisthacanthid material described here was obtained were initially sorted into scorpion and non-scorpion cuticles. The scorpion cuticle

was further sorted according to characteristics of the cuticle surface texture, the style and distribution of ornament, setation, colour, and refractivity (brightness) of the cuticle.

Palaeopisthacanthid-like cuticle was then sorted according to sclerite type, and these groups carefully studied to determine how many forms of each sclerite type are present. At this stage morphological differences due to intraspecific variation, ontogeny, sexual dimorphism, and taphonomic effects, may all be present. For reasons of parsimony, it is assumed that only one species is present at each locality, unless differences exist between sclerites which cannot be attributed to any of the factors responsible for variation cited above.

The Lone Star Lake assemblage, for example, contains three forms of pedipalp chelae, which for reasons discussed below are each believed to represent a separate species. Although differences do exist between specimens in other sclerite groups (e.g. femora, Pl. 5, figs 7, 9–10), they include characters such as cuticle thickness, the relative proportions of sclerites, and surface ornament distribution, which are all likely to vary intraspecifically, from somite to somite on a single individual, through ontogenetic development, and also due to sexual dimorphism. It was therefore not possible with the limited amount of material available to sub-divide the sclerite groups reliably, and for this reason all other specimens in the assemblage are provisionally assigned to the most common species (one chela form is presented by 11 specimens, the other two are based on single specimens). In the English Upper Carboniferous assemblages, no good grounds were found for sub-dividing any of the sclerite groups, so all material in each assemblage is attributed to a single species.

Once the minimum possible number of species represented in an assemblage has been determined and the general characteristics of those species identified, each assemblage was compared with the others to establish if one species was present in more than one assemblage. Finally, the collection as a whole was compared with available body fossils to try and identify any previously described forms. This procedure conforms with the recommendations made by Bengtson (1985) for sclerite-based taxonomy.

COMPARISON WITH BODY FOSSILS

Scorpion body-fossils are frequently well preserved compared with those of other terrestrial arthropods, but nevertheless taphonomic effects can make the remains very difficult to interpret. Characters employed in the taxonomy and systematics of fossil scorpions have tended to be those relating to gross body form, such as the structure of the coxosternal region, carapace shape, abdominal plate structure and the relative proportions of various body parts. Although the dispersed cuticle material is very well preserved, its fragmentary nature means that many of these taxonomically useful characters cannot be determined. Comparisons between body fossils and dispersed cuticles are therefore not easily made.

It is, however, possible to build up a set of characters observed in fragmentary material from an assemblage which can be used as a basis for comparisons. For the material under consideration, these are as follows:

1. The largest specimens, presumably from adults, come from scorpions with an estimated length of < 50 mm. This is unusually small for adult Carboniferous scorpions, several of which reached 300 mm in length.
2. All of the sternite fragments recovered have round intrasternite stigmata.
3. Trichobothrial follicles are present on the pedipalp femur, patella, and manus.
4. Lateral eye groups are reduced to a cluster of isolated lenses.
5. Median eyes are posterior to the lateral eyes.

Palaeopisthacanthus schucherti Petrunkevitch, 1913, is the only Palaeozoic scorpion which is known to have unequivocal intrasternite stigmata (Vogel and Durden 1966), and with *Compsoscorpheus elegans* Petrunkevitch, 1949, it has reduced lateral eye clusters and posteriorly displaced median eyes. Kjellesvig-Waering (1986) noted the occurrence of trichobothria in *Palaeopisthacanthus*, but the pedipalps of *Compsoscorpheus* are incompletely known and he was unable to determine whether trichobothria are present.

An examination of the available body fossils has confirmed Kjellesvig-Waering's observations. More importantly, small fragments of tergite cuticle are still present in the type material of *Compsoscorpis*, and this is identical in its cuticle characteristics to the material described here. *Palaeopisthacanthus* lacks preserved cuticle, but an excellent mould of the cuticle surface is present in the holotype, and it is clearly also of the same type. Kjellesvig-Waering (1986) did not note the similarity of cuticle ornament in *Palaeopisthacanthus* and *Compsoscorpis*. *Palaeopisthacanthus* is from the Mazon Creek fauna of Illinois. The fauna occurs in iron carbonate rich nodules from the Francis Creek Shale Member of the Carbondale Formation. Underlying the Francis Creek Shale is the Colchester (no. 2) Coal seam, and samples of the coal have yielded an abundant scorpion cuticle assemblage. Fragments of palaeopisthacanthid-type cuticle occur along with material attributable to several other Mazon Creek taxa.

Kjellesvig-Waering (1986) considered that *Palaeopisthacanthus* could be distinguished from *Compsoscorpis* on the basis of the shape of its carapace anterior margin. However, this structure is poorly preserved in all of the body fossils, so *Compsoscorpis elegans* Petrunkevitch, 1949, could justifiably be considered a junior synonym of *Palaeopisthacanthus schucherti* Petrunkevitch, 1913, with the minor differences between specimens noted by Kjellesvig-Waering (1986) possibly being due to intraspecific variation. However, the three known body-fossils of *C. elegans* all derive from a nodule fauna found c. 3 m above the Staffordshire Thick (or Main) Coal, in the Coseley district of England. The fauna is of Westphalian B age. Only one palaeopisthacanthid species was recognized in the English Carboniferous cuticle assemblages, also mostly of Westphalian B age, and since its trichobothrial distribution differs significantly from that of *P. schucherti*, the most parsimonious course of action available is to assign English palaeopisthacanthid material to *C. elegans*.

The Lone Star Lake assemblage from Kansas contains three species with palaeopisthacanthid-type cuticle. The most abundant of them has a trichobothrial distribution identical (as far as it is known) to *Compsoscorpis*, but other characters suggest that it does not belong in that genus, therefore it is described below as *Cryptoscorpis americanus* gen. et sp. nov. The other species are represented by single specimens of the pedipalp manus and fixed finger. One of these has been attributed to a new species of *Palaeopisthacanthus*, and the other has a number of unique characters which exclude it from any of the genera cited above, and is therefore described here as *Corniops mapezii* gen. et sp. nov.

PHYLOGENETIC RELATIONSHIPS

Previous work

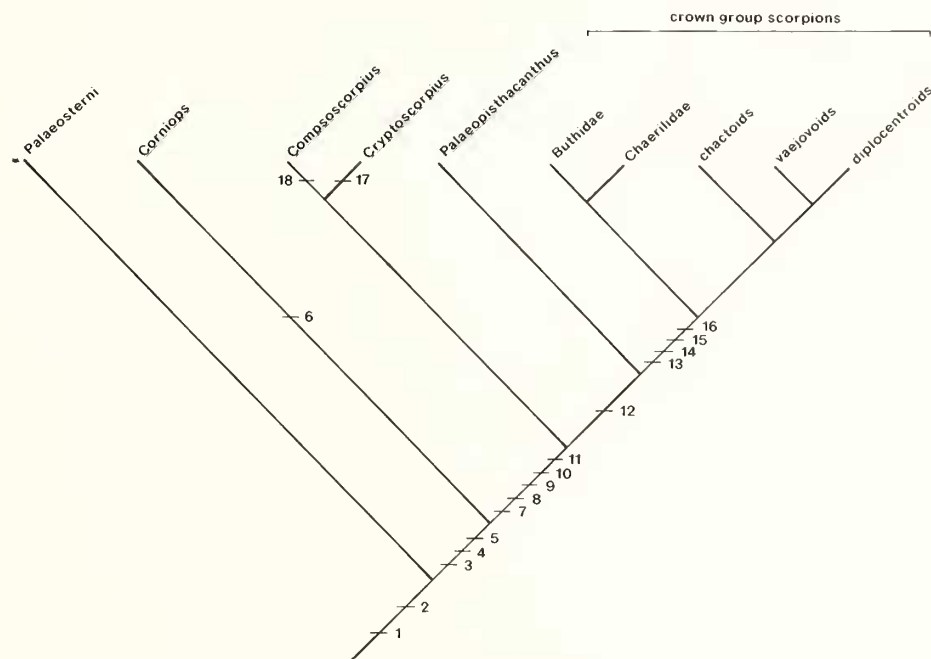
Kjellesvig-Waering (1986) placed the Palaeopisthacanthidae in his sub-order Neoscorpionina, primarily because he believed them to be the only Palaeozoic scorpions with book-lungs rather than gills, but also because he observed just three ocelli in each lateral eye group. However, it has been argued on the basis of functional morphology and palaeophysiology that most Palaeozoic scorpions were fully terrestrial and possessed book-lungs (Selden and Jeram 1989; Stockwell 1989). Direct evidence of book-lungs in a Lower Carboniferous scorpion which lacks intrasternite stigmata has also been described (Jeram 1990).

Stockwell (1989) sought to integrate the systematics of fossil and Recent scorpions, which had developed largely independently of each other. In doing so, he expanded the Neoscorpionina to include fossil forms with reduced lateral eye groups and with the two posterior pairs of coxae abutting the sternum. He achieved this by creating a new infraorder, the Palaeosterni, which essentially consists of the Eoctonoidea (*sensu* Kjellesvig-Waering 1986). The Palaeosterni lack intrasternite stigmata, but Stockwell (1989) followed Kjellesvig-Waering, and others, in assuming that they had marginal stigmata, although there is no convincing evidence that they are present in any eoctonoid (Wills 1960; Selden and Jeram 1989). Stockwell (1989) considered *Palaeopisthacanthus* and *Compsoscorpis* to be genera *incertae sedis* within the infraorder Orthosterni, in which were also included the four Recent superfamilies he recognized; the Buthoidea, Chactoidea,

Vaejovoidea, and Scorpionoidea. Stockwell's (1989) revision of Recent scorpion classification was based on an exhaustive cladistic analysis of all non-buthid genera, employing 138 binary characters. His conclusions differ from those of less thorough cladistic treatments (e.g. Lamoral 1980), but it remains to be seen if they will be widely accepted by neontologists.

Cladistic analysis

New characters revealed by the palaeopisthacanthid-type cuticles allow the position of this group to be determined relative to the Recent superfamilies. The cladogram given in Text-figure 1 is based on that of Stockwell (1989, fig. 251), but additional characters supporting the proposed palaeopisthacanthid groupings are supplied. Synapomorphies for the groupings of Recent scorpions are provided by Stockwell (1989) and are not repeated here. It should be noted that *Palaeopisthacanthus*, *Compsoscorpius*, and *Cryptoscorpius* gen. nov. are incompletely known, whilst *Corniops* gen. nov. is represented by a single pedipalp manus. Since it is the relationship between the palaeopisthacanthids and Recent scorpions that is of interest, only characters which might shed light on that relationship are considered here. *Gymmoscorpius* gen. nov. is not included in the cladogram.



TEXT-FIG. 1. Cladogram illustrating relationships between fossil orthostern taxa and Recent scorpion clades. Numbered autapomorphies supporting the groupings of taxa in the cladogram are discussed in the text.

The Palaeosterni are regarded as the sister group of the Orthosterni and recognition of autapomorphies for the suborder (Paleosterni + Orthosterni) was achieved by outgroup comparison with all other Palaeozoic scorpions. The Orthosterni show three important character state transition series which provide most of the taxonomically useful character states listed below:

1. Reduction of number of ocelli in lateral eye groups.
2. Increase in trichobothrial numbers.
3. Reduction in number of cheliceral teeth (reversal).

Particular emphasis is placed on trichobothrial character states because of their importance in Recent scorpion taxonomy (Sissom 1990), and the variability of this character in the fossil material.

Discussion of characters

The characters employed are listed below and followed by the plesiomorphic state, the derived state, and a brief discussion of each character.

1. Lateral ocelli (a): 'compound' lateral eyes, or, dispersed lateral ocelli, with ten or fewer ocelli in each lateral eye group. 'Compound' lateral eyes like those of eurypterids occur in all Palaeozoic scorpions except the Neoscorpionina, in which the eyes are reduced to ten or fewer isolated ocelli. Preservation rarely allows the lateral eyes to be studied in detail, and although many fossil scorpions appear to lack them (Petrunkevitch 1949; Kjellesvig-Waering 1986), their loss has only been conclusively demonstrated in some Triassic mesophonids (Wills 1947).

2. Preanal segment: short, or, long. Palaeosterni and Orthosterni have a preanal segment which is significantly longer than the preceding metasomal segment. In all other fossil scorpions the preanal segment is shorter than, or approximately equal in length to, the preceding metasomal segment.

3. Cuticle ornament: non-palaeopisthacanthid-type, or, palaeopisthacanthid-type.

4. Chelal trichobothria (a): trichobothria absent, or, trichobothria present. The presence of pedipalpal trichobothria is regarded here as a synapomorphy for the Orthosterni (*Corniops* gen. nov., + palaeopisthacanthids + Recent families). They have not been positively identified in any other fossil scorpions.

5. Pedipalp dentition (a): palaeostern-type, or, orthostern-type. The pedipalp dentition of modern scorpions and palaeopisthacanthids consists of simple thorn-like teeth arranged in rows along the opposed faces of the pedipalp fingers. With the exception of juveniles, in which the dentition is similar to that of Recent scorpions (unpublished observations), all other fossil scorpions in which dentition is known have rows of large follicles, within which are set sclerotised conical teeth (see Wills 1947, pl. 9, figs 1–6; 1960, pl. 50, fig. 3). The dentition of orthostern-type may have been derived by the neotenic retention of juvenile palaeostern dentition in orthostern adults.

6. Pedipalp dentition (b): main denticle row divided into primary sub-rows, or, single continuous denticle row. The Palaeosterni, Palaeopisthacanthidae, and nearly all Recent scorpions, have a main denticle row composed of discrete primary sub-rows. The single continuous denticle row of *Corniops* gen. nov. is therefore probably an autapomorphy for that genus.

7. Cheliceral dentition (a): no internal teeth, or, five internal teeth. Cheliceral dentition is a taxonomically useful character in Recent scorpions (Vachon 1963) but the preservation of fossils is rarely good enough for their dentition to be described accurately. However, the cheliceral dentition of palaeopisthacanthids is unique among scorpions, living or fossil. The presence of five internal teeth on the fixed finger is a palaeopisthacanthid autapomorphy. Internal teeth are unknown in other fossil scorpions, but a single internal tooth is present in Recent buthids, and a pair in some chactoids. A character state transition series leading to the reduction of cheliceral teeth on both the fixed and movable fingers could account for the states present in each of the Recent scorpion families. It is also notable that the palaeopisthacanthid state, plesiomorphic with respect to Recent families (Stockwell 1989), shows little size differentiation of teeth. The notation developed by Vachon (1963) for cheliceral dentition assumes the homology of certain teeth in different families. However, if Recent scorpion dentitions have been derived by reduction in number and size differentiation from the plesiomorphic state, then the assumption of homology should be viewed with caution, and it may be necessary to reassess cheliceral dentition in Recent families in the light of fossil evidence.

8. Lateral ocelli (b): lateral ocelli all approximately of same size, or, major and minor ocelli present. Lateral ocelli of palaeopisthacanthids and some Recent scorpions show size differentiation

into major and minor ocelli (Text-fig. 8B; González-Sponga 1977). Size differentiation has not been observed in other fossil scorpions or eurypterids.

9. Intrasternite stigmata: absent, or, present. Intrasternite stigmata are present in all Recent scorpions and palaeopisthacanthids. Marginal stigmata are known in *Mesophonus* (*sensu* Wills 1947), and have been postulated in some Palaeozoic scorpions (Kjellesvig-Waering 1986). However, none of the Palaeozoic cases is convincing, and where the ventral mesosomal anatomy is well known, stigmata are certainly absent (Wills 1960). The presence of intrasternite stigmata is therefore a synapomorphy for the Palaeopisthacanthidae + Recent families, and the marginal stigmata of *Mesophonus* are almost certainly independently derived (see also Jeram 1994).

10. Chelal trichobothria (b): pedipalp manus lacking Et trichobothria, or, pedipalp manus with Et trichobothria.

11. Metasomal segments: Anterior transverse ridge absent, or, anterior transverse ridge present. Metasomal segments of palaeopisthacanthids all have an anterior transverse ridge (like that present on mesosomal tergites) around the circumference of the sclerite. A limited survey of Recent scorpions revealed that it is present in some genera (e.g. *Ananteris*, *Lychas*, *Euscorpius*, *Pandinus*) but only on the ventral surface of the first, and sometimes second, metasomal segment. In other genera (e.g. *Broteochactus*) it is absent. This character is not present in the Palaeosterni, or in other fossil scorpions where the metasoma is known in detail, and therefore is a synapomorphy for the Palaeopisthacanthidae + Recent families.

12. Chelal trichobothria (c): No Eb trichobothria on manus, or, two or more Eb trichobothria on manus. The addition of Eb trichobothria on the manus of *Palaeopisthacanthus* is shared with all Recent scorpions, where there are three Eb trichobothria in each of the fundamental patterns.

13. Cheliceral dentition (b): Five internal teeth on fixed finger, or, one or none internal teeth (reversal). See notes for character 7 above.

14. Lateral ocelli (c): more than five lateral ocelli, or five or fewer lateral ocelli. Recent scorpions have two to five lateral ocelli in each lateral eye group. This reduction in number serves as a synapomorphy for the Recent scorpion families.

15. Chelal trichobothria (d): only eb trichobothrium on fixed finger, or, trichobothria present on fixed finger in addition to eb. Vachon (1973) recognized three 'fundamental' patterns of trichobothrial distribution in Recent scorpions. The three 'fundamental' patterns themselves share an underlying pattern common to them all which, it might be reasonably hypothesized, represents the plesiomorphic state with respect to the Recent scorpion families. Using the notation proposed by Vachon (1973), the following chelal trichobothria are common to all three distributions; Eb₍₁₋₃₎, V₁, Et, Est, Esb, it, db, dt, et, est, eb, esb. The overall polarity of this character state transition series is toward the addition of trichobothria, although rare trichobothrial losses are also known (e.g. Franke and Soleglad 1981). The palaeopisthacanthid pattern is very much less derived than any of the modern chelal distributions. Furthermore, the latest common ancestor of all modern scorpion families probably also had a considerably more derived chelal pattern than the palaeopisthacanthids. The hypothetical distribution for this ancestor is; Eb₍₁₋₃₎, Esb, Est, Et, V₍₁₋₄₎, it, ib, db, dt, et, est, eb, esb. From this, the type A pattern (Buthidae) could be derived by the loss of V₍₃₋₄₎ and ib; the type B pattern (Chaerilidae) by the loss of V₍₂₋₄₎; and the type C pattern (all other Recent families) by the addition of Et₍₂₋₄₎, Dt, Dst, and dsb.

It might be argued that either the type A or type B pattern is the most primitive, and that the others are derived from it, but as the palaeopisthacanthids possess four ventral trichobothria on the manus, this should be regarded as the plesiomorphic state, and the loss of ventral trichobothria is a derived state in the Buthidae and Chaerilidae. Furthermore, it would be a very remarkable case of parallelism indeed if all three Recent distributions were derived independently from a palaeopisthacanthid-type distribution, since with fourteen common trichobothria there is a high degree of congruency between them. Although these arguments have only been applied to the chelal trichobothria, similar cases can be made for the derivation of femoral and patellar trichobothria. For the purposes of this analysis, the derived state is most simply characterized by the presence of trichobothria on the fixed finger, in addition to the eb trichobothrium.

16. First mesosomal sternite: short, or, long. In palaeopisthacanthids and the Palaeosterni the first mesosomal sternite is shorter than the second. All Recent scorpions have a sub-trapezoidal first sternite which is longer than the more rectangular second sternite.

17. Pedipalp fingers: longer than manus, or, equal to manus. In the plesiomorphic state the pedipalp fingers are longer than the manus. In *Cryptoscorpis* gen. nov. the fingers are approximately equal in length to the manus. Although many Recent genera have short fingers, this character appears to have originated independently many times, and in this case it can be regarded as an autapomorphy for *Cryptoscorpis* gen. nov. within the Palaeopisthacanthidae.

18. Pedipalp secondary structures: absent, or, present. The presence of a tubercular secondary structure on the external face of the pedipalp manus in *Compsoscorpis* is regarded as an autapomorphy for the genus. Similar structures occur on the internal face in most Recent bothrid males (Maury 1975), but they are not homologous and were independently derived.

Discussion. Results of the analysis are summarized in Text-figure 1. *Palaeopisthacanthus* emerges as the most crownward of the stem group plesions by virtue of the Eb trichobothria on its pedipalp manus, and an additional probable Et trichobothrium. The increased number of trichobothria on the pedipalp femur noted in one specimen (K14426) supports this, although only characters visible in the holotype of *P. schucherti* were utilized in the analysis. No uniquely derived characters were recognized in *Palaeopisthacanthus*. The other Carboniferous orthosterns are even more plesiomorphic with respect to the Recent scorpions. *Compsoscorpis* and *Cryptoscorpis* gen. nov. share a common trichobothrial distribution. Together they comprise the *Compsoscorpis* plesion. The genera are each supported by autapomorphies, but again the plesion as a whole has no uniquely derived characters. The position of *Corniops* gen. nov. as the least crownward plesion is determined by the apparently plesiomorphic state of its trichobothrial type and distribution. However, since only the partial pedipalp manus and fixed finger are currently known, it may ultimately be demonstrated that four of the five synapomorphies shared by the more crownward taxa were also shared by *Corniops* gen. nov. If this were the case, it would still not effect the position of *Corniops* gen. nov. as the most plesiomorphic of the orthosterns. The pedipalpal dentition of *Corniops* gen. nov. is an autapomorphy of the genus. Synapomorphies supporting the groupings of Recent families and superfamilies in the cladogram are given by Stockwell (1989).

For the time being it is convenient to reserve the Carboniferous family Palaeopisthacanthidae, in which *Palaeopisthacanthus*, *Compsoscorpis*, and *Cryptoscorpis* gen. nov. are included, even though these genera do not share any uniquely derived characters. It would however not be appropriate to assign *Corniops* gen. nov. to the Palaeopisthacanthidae, or to establish a new family to accommodate it.

What is clear from the cladogram is that none of the Carboniferous orthosterns could be included in the crown group because the hypothetical last common ancestor of all Recent scorpions would have been significantly more derived than *Palaeopisthacanthus*. It is probable therefore that the crown group originated after the Late Carboniferous, but biogeographical evidence for the timing of origins of major Recent scorpion clades is somewhat ambiguous (e.g. Lamoral 1980; Stockwell 1989). The occurrence of palaeopisthacanthid-type cuticle fragments in Dinantian age shales overlying the East Kirkton Limestone at Bathgate, Scotland, pushes the probable origin of the orthostern scorpions back at least as far as the Early Carboniferous (Jeram 1994). Material which may represent a much older orthostern is present in the Middle Devonian Gilboa assemblage, but further study will be required to confirm the identity of these fragments.

At present no consensus exists amongst arachnologists concerning the systematic position of scorpions within the Chelicerata. However, in recent years there has been a general recognition that the class Arachnida is polyphyletic (Firstman 1973; Van der Hammen 1977; Weygoldt and Paulus 1979). Stockwell (1989) followed Van der Hammen (1977) in raising the Scorpionida to the status of a class. As a consequence more space is available in the taxonomic hierarchy for the grouping of fossil forms into monophyletic clades, thereby facilitating the integration of fossil and Recent scorpion classifications. In spite of the work of Kjellesvig-Waering (1986), there is still a long way

to go before the systematics of fossil scorpions can be regarded as satisfactory. In the meantime the Palaeopisthacanthidae are not referred to any higher taxon within the Orthosterni, although it is hoped that the recognition and description of these plesiomorphic stem group taxa will facilitate a re-examination of Recent scorpion relationships and ultimately stabilization of their systematics.

SYSTEMATIC PALAEOONTOLOGY

Class SCORPIONIDA Latreille, 1810

Order SCORPIONES Hemprich and Ehrenberg, 1837

Suborder NEOSCORPIONINA Thorell and Lindström, 1885

Infraorder ORTHOSTERNI Pocock, 1911

Emended diagnosis. Neoscorpionina with intrasternite stigmata. Pedipalpal trichobothria present.

Family PALAEOPISTHACANTHIDAE Kjellesvig-Waering, 1986

Emended diagnosis. Orthosterni with four ventral trichobothria on the pedipalp manus, only eb trichobothrium on pedipalp fixed finger.

Genus PALAEOPISTHACANTHUS Petrunkevitch, 1913

Type species. *Palaeopisthacanthus schucherti* Petrunkevitch, 1913, from the Upper Carboniferous (Westphalian D) Francis Creek Shale of the Mazon Creek area, Illinois.

Emended diagnosis. Palaeopisthacanthidae with at least two Eb trichobothria on the pedipalp manus. Pedipalp fingers longer than manus.

Palaeopisthacanthus schucherti Petrunkevitch, 1913

Text-figure 2

1913 *Palaeopisthacanthus schucherti* Petrunkevitch, p. 48, pl. 2, figs 8–9; text-figs 11–12.

1949 *Palaeopisthacanthus schucherti* Petrunkevitch; Petrunkevitch, p. 154.

1953 *Palaeopisthacanthus schucherti* Petrunkevitch; Petrunkevitch, p. 33.

1955 *Palaeopisthacanthus schucherti* Petrunkevitch; Petrunkevitch, p. 43, text-fig. 43.

1966 *Palaeopisthacanthus schucherti* Petrunkevitch; Vogel and Durden, p. 655, pl. 81, figs 1–3; text-figs 1–2.

1986 *Palaeopisthacanthus schucherti* Petrunkevitch; Kjellesvig-Waering, p. 232, text-figs 103–104.

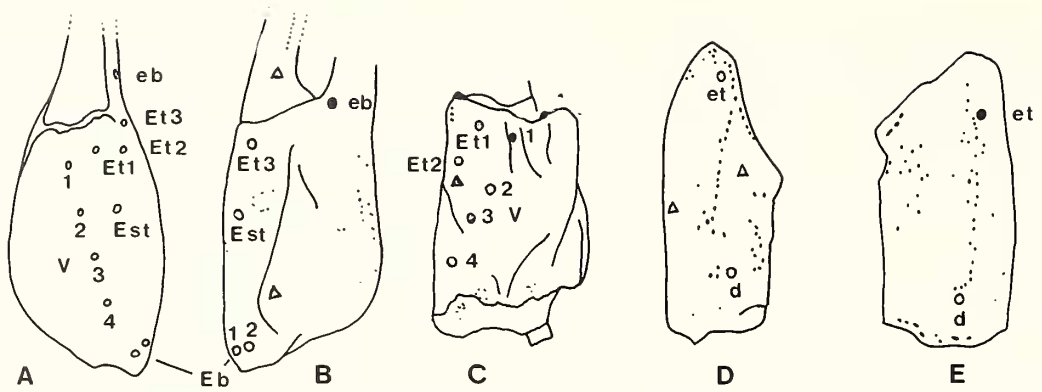
Holotype. Part and counterpart of a small ironstone nodule, YPM 140, containing the mould of a partially preserved scorpion, from the Francis Creek Shale of the Mazon Creek area, Grundy county, Illinois.

Additional material. See Appendix 1.

Emended diagnosis. As for genus, with three Et trichobothria positioned close to external condyle

Discussion. The description of the holotype given by Kjellesvig-Waering (1986) was found to be reasonably accurate. However, several significant characters are redescribed here based on a re-examination of the holotype and additional material from the Colchester (no. 2) Coal (locality 7). Most aspects of Kjellesvig-Waering's (1986) description were confirmed, and are not repeated here.

Carapace. Kjellesvig-Waering (1986, p. 232) diagnosed *Palaeopisthacanthus* as having a 'strongly-cuspidate anterior margin'. The appearance of a cuspidate anterior margin may be illusory, due to the bowing of the carapace anterior margin over the chelicerae in the fossil. The carapace shape is similar to that of *Cryptoscorpis* gen. nov. and *Compsoscorpis*. Vogel and Durden (1966) correctly



TEXT-FIG. 2. *Palaepithacanthus schucherti* Petrunkevitch, 1913. YPM 140, holotype; Francis Creek Shale (Westphalian D); Mazon Creek, Illinois. A, reconstruction of chelal trichobothrial distribution, viewed from inferior side. B, left chela, exterior surface. C, left chela, interior surface. D, left pedipal patella, superior surface. E, right pedipalp femur, superior surface. Figures B-E after Kjellesvig-Waering (1986, text-fig. 104). In figures B-E, triangles indicate trichobothria identified by Kjellesvig-Waering but not confirmed by this study; filled circles are trichobothria not noted by Kjellesvig-Waering; open circles are trichobothria noted by Kjellesvig-Waering and confirmed in this study.

observed three large lateral ocelli on each side of the carapace. These are located on raised eye nodes, and it is possible that minor ocelli are also present, but cannot be reliably differentiated from cuticular tubercles in the mould.

Coxal apophyses. The apophyses of the first two pairs of walking-leg coxae are not well-preserved in the holotype. The anterior tips of both pairs have broken away, and what appeared to Kjellesvig-Waering (1986) to be a *Chaerilus*-like spatulate apophysis on the anterior coxa is probably part of the underlying pedipalpal coxa. A pair of apophyses from the Colchester (no. 2) Coal (K14422) are identical in structure to those of *Cryptoscorpis* gen. nov. (Pl. 6, fig. 1; Text-fig. 8A).

Sternum. Kjellesvig-Waering (1986, text-fig. 103) interpreted the sternum as occupying the entire area between the three posterior pairs of coxae. However, an alternative interpretation of the fossil is possible. The illustrations of Vogel and Durden (1966, pl. 8, fig. 2; text-fig. 2) show a convex anterior margin which is easily visible in the specimen. The triangular area anterior to this which Kjellesvig-Waering (1986) interpreted as an anterior portion of the sternum may simply be due to the post-mortem separation of the second pair of coxae. If this interpretation is correct, then the sternum is sub-pentagonal with convex anterior and lateral margins, and is wider than long.

Sternites. Vogel and Durden (1966) found only three stigmata-bearing sternites on the ventral surface of the abdomen. Kjellesvig-Waering (1986) reported a fourth sternite anterior to these, although the presence of stigmata on the anterior sternite was not confirmed by this study because

EXPLANATION OF PLATE I

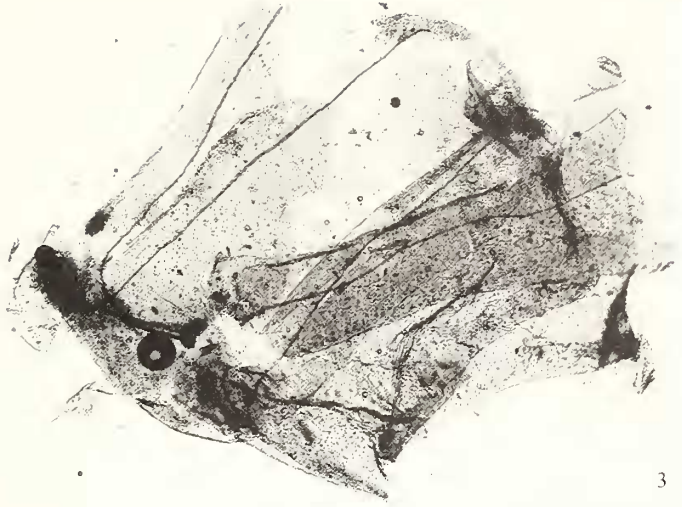
Figs 1-9. *Composcorpis elegans* Petrunkevitch, 1949. See Appendix 1 for localities. All specimens Upper Carboniferous (Westphalian B). 1, K14475; mesosomal tergite 5 from same specimen as figure 3; $\times 26$. 2, K14504; posterior mesosomal tergite; $\times 26$. 3, K14475; partial mesosoma; see Text-figure 3A for explanation; $\times 26$. 4, K14433; postabdominal segment; see Text-figure 3C for explanation; $\times 26$. 5, K14472; right side of sternite; see Text-figure 3F for explanation; $\times 4$. 6, K14533 sternite fragment; see Text-figure 3D for explanation; $\times 42$. 7, K14481; preanal segment; see Text-figure 3B for explanation; $\times 26$. 8, K14570; postabdominal segment, ventral surface in centre; see Text-figure 3E for explanation; $\times 26$. 9, K14517; see Text-figure 3G for explanation; $\times 26$.



1



2



3



4



6



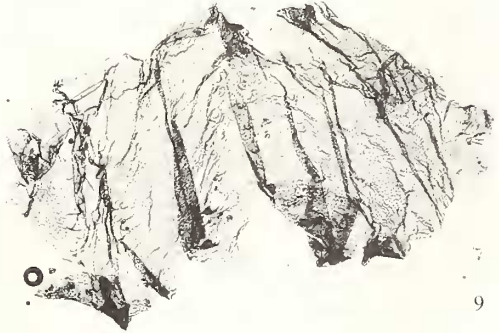
7



5



8



9

JERAM, *Compsoscorpius*

preservation in this area of the holotype is poor. The anterior sternite is very short, contrasting with Recent scorpions, in which the anterior sternite is elongated relative to the others.

Pedipalps. Kjellesvig-Waering (1986) stated that the pedipalp fingers lack denticles, but a row of denticles can be seen towards the base of the free finger of the left pedipalp of the holotype. The apparent absence of dentition on the fingers is due to post mortem distortion and folding of the cuticle which has obscured the cutting edges almost entirely. Trichobothrial follicles (bothria) are preserved as mushroom-shaped bosses on the internal mould, due to sediment infilling the cup-like bothria. Setal follicles are much smaller, and are preserved as simple round scars on the mould. The trichobothrial distribution of *P. schucherti* is shown in Text-figure 2. Most of the bothria noted by Kjellesvig-Waering (1986) were confirmed, but a few features are definitely not bothria, some are equivocal, and a few additional bothria were located. The pedipalp femur of the holotype reveals a single d bothrium, and a possible et bothrium. The patella also has one d and one et bothrium. Two other bothria figured by Kjellesvig-Waering (1986, text-fig. 104E) could not be located with certainty. Chelal trichobothria are similar to those of other palaeopisthacanthids described below, with some additions. Four ventral, three Et, and two Eb bothria are present. An additional Eb bothrium may have been present in life, but the crumpled preservation of the holotype's cuticle surface means that it is unlikely that all the original trichobothria will be determinable, particularly on the poorly preserved left pedipalp. Two bothria figured by Kjellesvig-Waering (1986) are inconclusive, and the supposed bothrium on the free finger is a large pyrite granule (Text-fig. 2B).

Palaeopisthacanthus vogelandurdeni sp. nov.

Plate 5, figure 4; Plate 7, figure 6; Text-figure 6D

Derivation of name. The species name is in honour of Beatrice Vogel and Christopher Durden who first recognized the close relationship of *Palaeopisthacanthus* to Recent scorpions.

Holotype. Fixed finger and distal portion of a pedipalp manus, K14086, from cuticular shales immediately overlying the Lower Williamsburg Coal, at Lone Star Lake, Kansas.

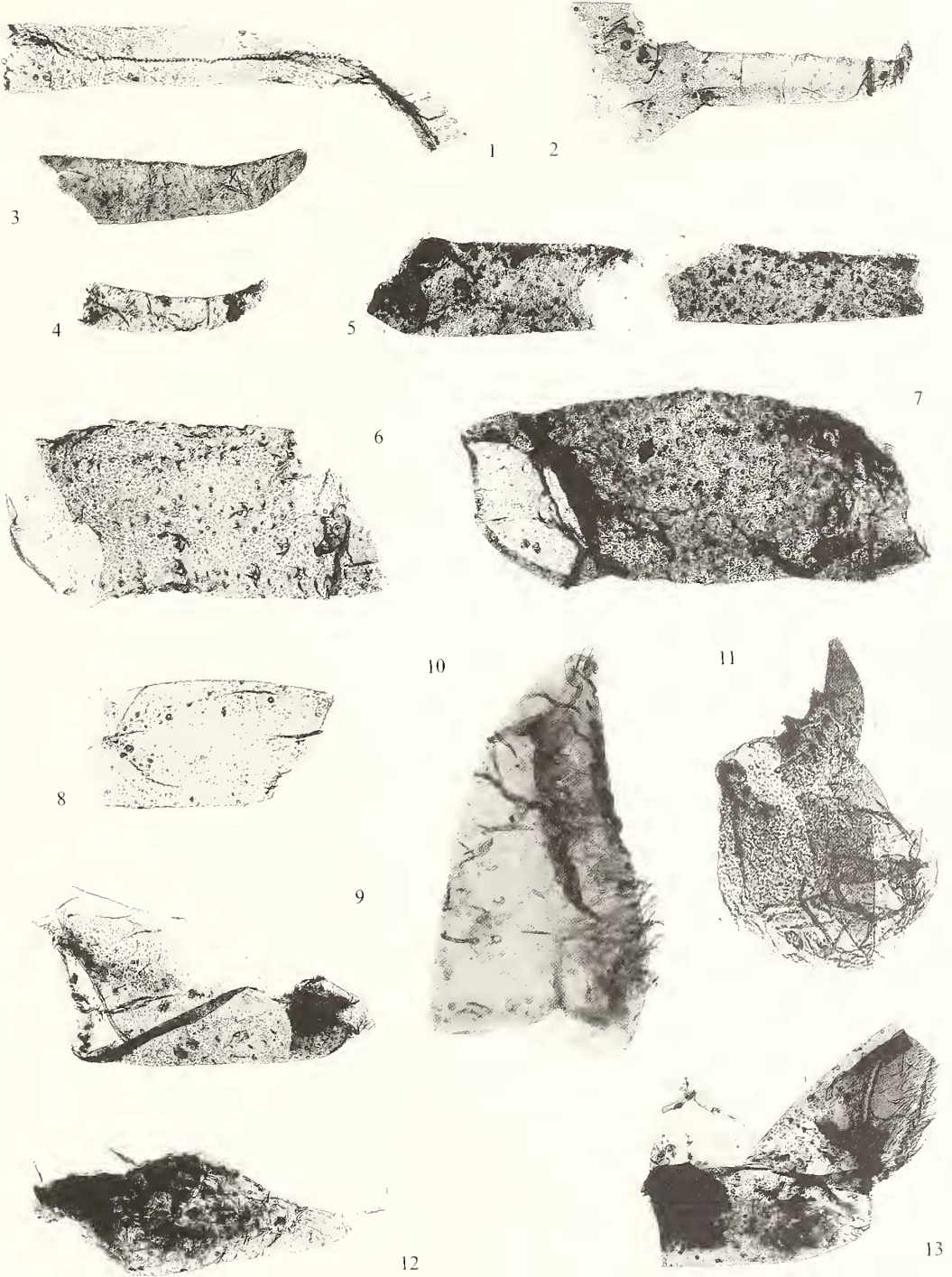
Additional material. The Lone Star Lake assemblage probably contains additional fragments belonging to this species, but at present they cannot be reliably differentiated from those of *Cryptoscorpium mapesii* gen. et sp. nov.

Diagnosis. Pedipalp fingers longer than manus. Primary denticle row consisting of seven primary sub-rows, each containing twelve to fourteen denticles. Et trichobothrium positioned approximately half way across the external face of the manus.

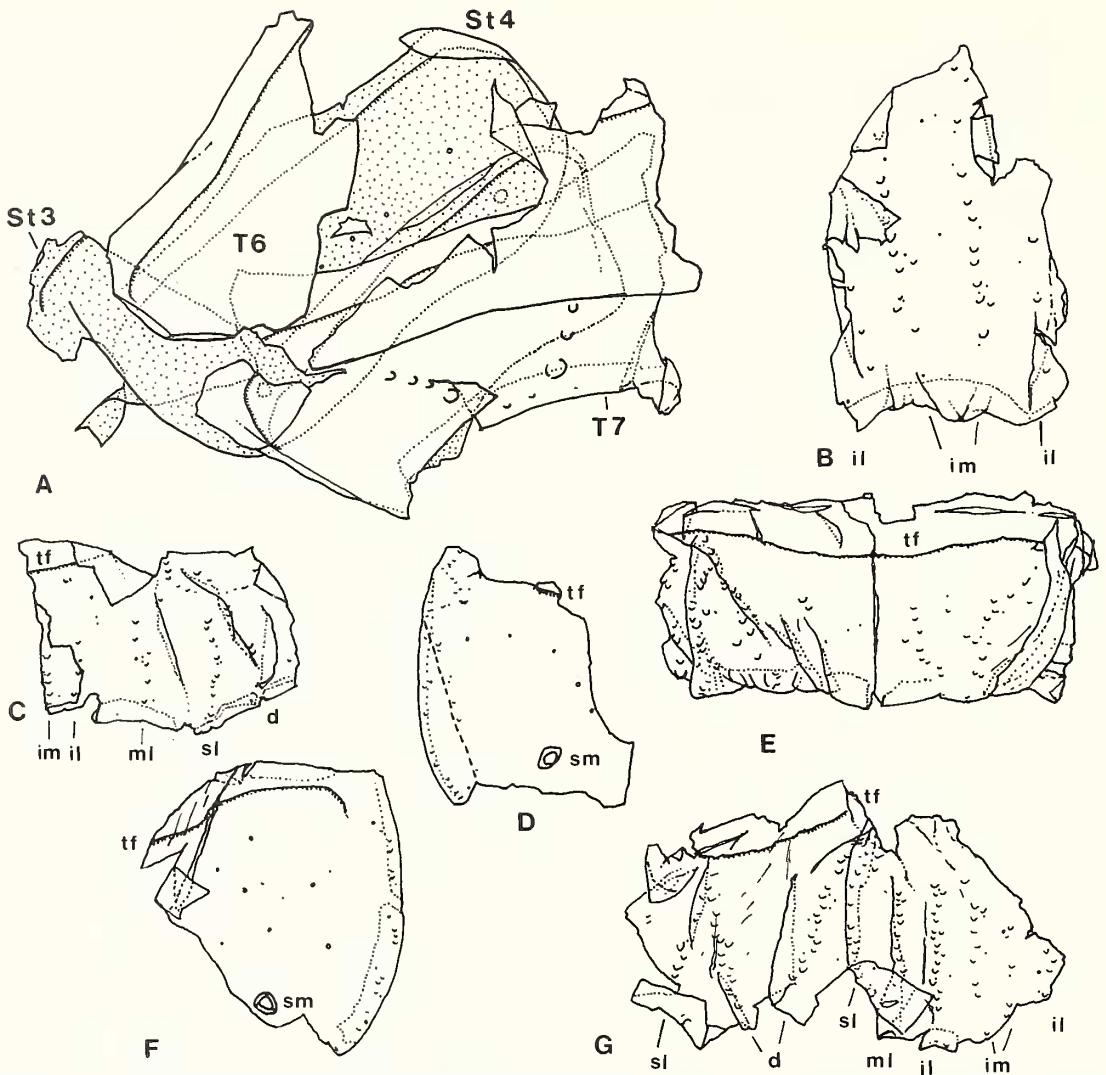
EXPLANATION OF PLATE 2

Figs 1–7, 10–13. *Compsoscorpium elegans* Petrunkevitch, 1949. See Appendix 1 for localities. 1–2, 4–7, Upper Carboniferous (Westphalian B); 3, Upper Carboniferous (Westphalian A). 1, K14485; pedipalp free finger; × 32. 2, K14490; partial pedipalp manus and fixed finger; see Text-figure 4A–B for explanation; × 32. 3, K14428; partial pedipalp finger; × 32. 4, K14500; juvenile pedipalp finger; × 32. 5, K14432; two fragments from an adult pedipalp free finger; × 26. 6, K14460; pedipalp patella; see Text-figure 3E for explanation; × 32. 7, K14566; adult pedipalp patella, see Text-figure 3C for explanation; × 26. 10, K14564; chelicera free finger, external row of teeth in centre; × 64. 11, K14546; 'chelicera' manus with fixed finger; see Text-figure 3E for explanation; × 42. 12, K14571; vesicle and aculeus, proximal end obscured by opaque organic matter; × 26. 13, K14499; coxa of walking-leg 2 with apophysis; × 32.

Figs. 8–9. *Cryptoscorpium americanum* gen. et sp. nov.; Lone Star lake, Kansas; Upper Carboniferous (Stephanian B). 8, K14402; juvenile pedipalp femur with three superior trichobothria; see Text-figure 3D for explanation; × 39. 9, K14098; coxa of walking leg 3; × 26.

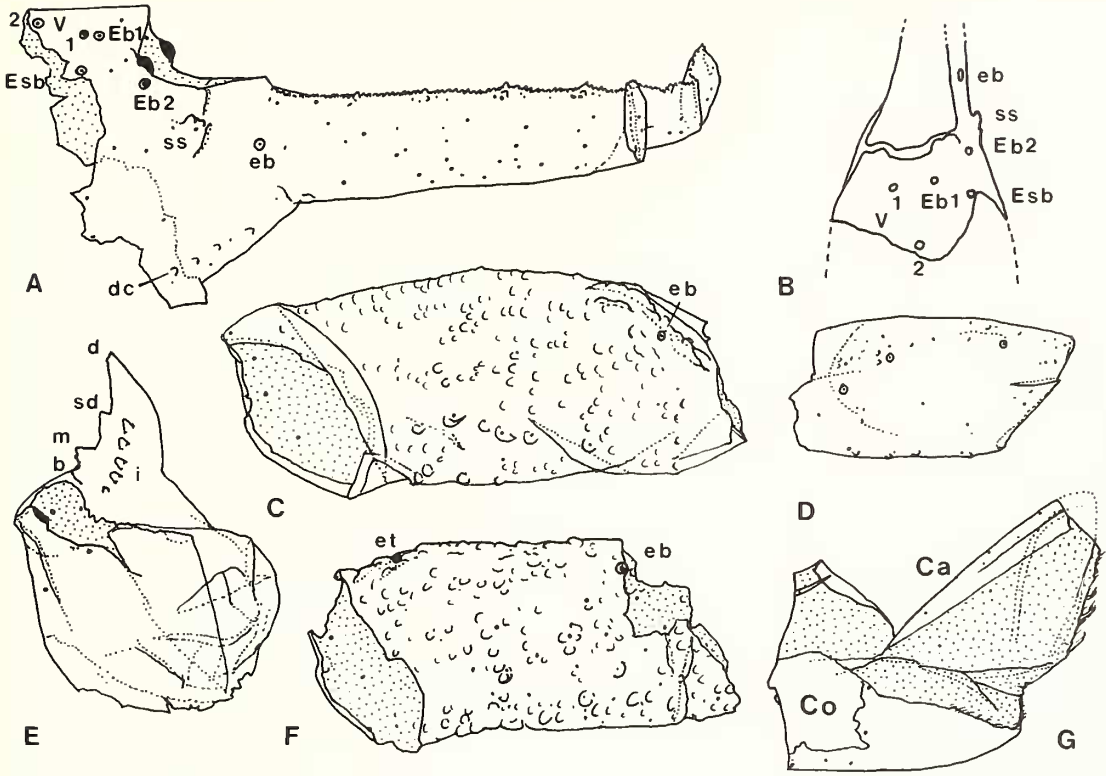


JERAM, *Compsoscorpius*, *Cryptoscorpius*



TEXT-FIG. 3. *Comptoscorpius elegans* Petrunkevitch, 1949. Explanatory drawings for specimens illustrated in Plate 1. All specimens from the Westphalian B of England; see Appendix for details of locality and horizon for individual specimens. See Plate 1 for scale. A, K14475; partial abdomen viewed from dorsal side; tergite 6 is torn into two large fragments and overlies tergite 7; these overly sternite 4, in which the right stigma is clearly visible; a small fragment of sternite 3 is present on the far left. B, K14481; ventral surface of preanal segment, showing inferior median and inferior lateral carinae. C, K14433; right half of metasomal segment opened out to display dorsal surface on right and ventral on left. D, K14533; fragment of large sternite, the folded lateral margin has been restored to its original position in the drawing. E, K14570; metasomal segment, opened out to display ventral surface in centre and dorsal surface on either side. F, K14472; sternite fragment viewed from ventral side. G, K14517; metasomal segment opened out to display dorsal surface on left and ventral on right. Abbreviations and conventions are given in 'Methods' in the text.

Description. The fixed finger is long and slender, and although only a distal portion of the manus is preserved it is clear that the finger was considerably longer than the manus in life, like that of *P. schurcherti*. The cuticle of the manus is finely tuberculate, but the distal two-thirds of the fixed finger lack ornament. A prominent dorso-interior marginal carina is present, and two further carinae are visible on the portion of the exterior



TEXT-FIG. 4. *Compsoscorpius elegans* Petrunkevitch, 1949 (A–C, E–G) and *Cryptoscorpius americanus* gen. et sp. nov. (D). Explanatory drawings for specimens illustrated in Plate 2. All specimens of *C. elegans* are from the Westphalian B of England; *C. americanus* gen. et sp. nov. is from Lone Star Lake, Kansas (Stephanian B). See Appendix for details of localities and horizons, and Plate 2 for scale. A, K14490; distal end of pedipalp manus and fixed finger, viewed from exterior side, dorsal surface at bottom. B, reconstruction of trichobothrial distribution on K14490; viewed from inferior side. C, K14566; pedipalp patella viewed from inferior prolateral side; et bothrium is not visible due to opaque detritus. D, K14402; pedipalp femur from juvenile with three superior bothria, viewed from superior side. E, K14546; cheliceral hand and fixed finger viewed from inner side. F, K14460; pedipalp patella viewed from inferior prolateral side, proximal end missing. G, K14499; coxa of leg 2 showing broad apophysis with filtering mat of setae, distal end missing, viewed from inner side. Abbreviations and conventions are given in 'Methods' in the text.

surface preserved (Pl. 5, fig. 4). Applying the nomenclature of Stahnke (1970), the superior of this pair is an inner secondary carina, and the inferior, a digital carina. Two bothria are present on the holotype. The eb bothrium is remarkable as the only example of palaeopisthacanthid trichobothrium in which the hair is still present (Pl. 5, fig. 4). The hair lies between the opposed layers of cuticle and owes its preservation to having been pushed inwards into the lumen of the sclerite. The other is an Et bothrium lying approximately half way across the external surface on the digital carina. Although the manus is incomplete, it is certain that no external trichobothria lie distally to this one on the manus, and therefore Et is the most appropriate designation for it. However, it must be borne in mind that Vachon's (1973) terminology was devised for describing trichobothrial distributions in Recent scorpions, and that the terminology may not be able to accommodate all the potential variations in fossil material.

The dentition of the fixed finger consists of slightly oblique non-imbricated primary sub-rows. Excluding the most proximal sub-row, which is not complete in the holotype, twelve to fourteen denticles are present in each sub-row, the basal denticle in each being the largest. An internal accessory denticle lies just proximally to the basal denticle of each sub-row. There are no supernumerary denticles (Pl. 7, fig. 6).

Discussion. The species is assigned to *Palaeopisthacanthus* because of its distinctive cuticle ornament and long pedipalp fingers. It can be distinguished from *P. schucherti* by the position of the Et trichobothrium. The absence of a secondary structure of the external face of the manus excludes it from *Compsoscorpius*.

Genus COMPSOSCORPIUS Petrunkevitch, 1949

Type species. *Compsoscorpius elegans* Petrunkevitch, 1949, from the Upper Carboniferous (Westphalian B) of Staffordshire, England.

Emended diagnosis. Palaeopisthacanthid with thirteen pedipalpal trichobothria, of which eight are chelal, three lie on the femur and two on the patella. Pedipalp fingers nearly twice the length of the manus. Chelal dentition of seven primary sub-rows, with twelve to fourteen denticles in each. Manus with large tubercular secondary structure on external face just posterior to the eb-trichobothrium.

Compsoscorpius elegans Petrunkevitch, 1949

Plate 1; Plate 2, figures 1–7, 10–13; Plate 3, figures 1–10; Plate 6, figures 4–7; Plate 7, figures 1, 5; Text-figures 3; 4A–C, E–G; 5A–J

- 1911 *Anthracoscorpio buthiformis* Pocock [*partim*], p. 26, fig. 7.
 1949 *Typhlopisthacanthus anglicus* Petrunkevitch, p. 145, figs 143, 182.
 1949 *Compsoscorpius elegans* Petrunkevitch, p. 149, figs 152, 154, 183–185.
 1949 *Compsoscorpius elongatus* Petrunkevitch, p. 150, figs 147–150, 186–188.
 1953 *Compsoscorpius elegans* Petrunkevitch; Petrunkevitch, p. 32.
 1953 *Compsoscorpius elongatus* Petrunkevitch; Petrunkevitch, p. 33.
 1953 *Typhlopisthacanthus anglicus* Petrunkevitch; Petrunkevitch, p. 34.
 1955 *Compsoscorpius elegans* Petrunkevitch; Petrunkevitch, p. 75, fig. 44.
 1986 *Compsoscorpius elegans* Petrunkevitch; Kjellesvig-Waering, p. 236, text-figures 105–107.
 1987 *Scorpionida incertae sedis* Bartram *et al.*, fig. 1.

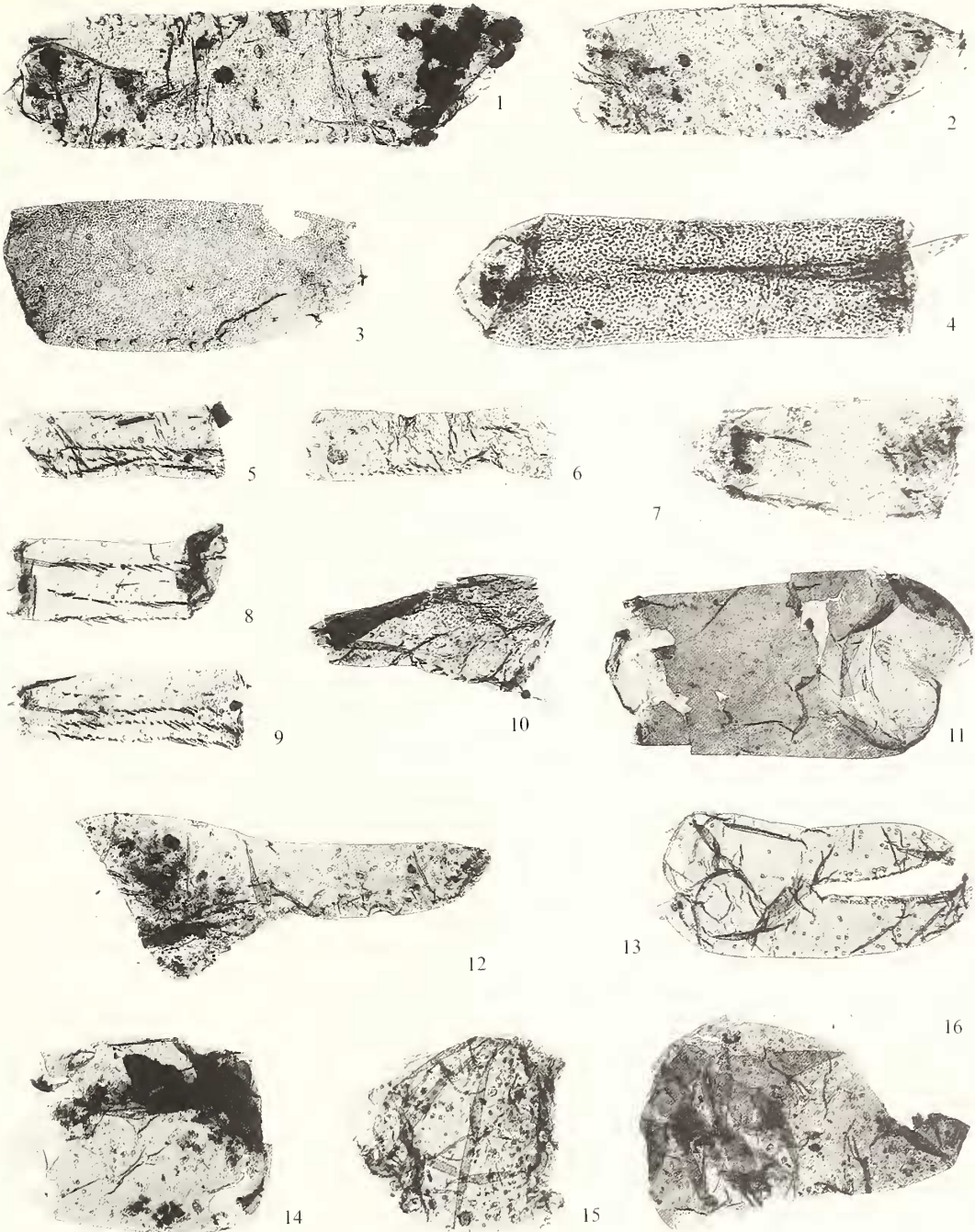
Holotype. BMNH I7883, part and counterpart of a small incomplete scorpion preserved in an ironstone nodule.

Additional material. BMNH In15862 and In31261. These are the holotypes of *C. elongatus* Petrunkevitch, and *Typhlopisthacanthus anglicus* Petrunkevitch respectively, which Kjellesvig-Waering (1986) considered to be junior synonyms of *C. elegans*. All three specimens are from shales above the Thick (or Main) Coal, in the Coseley district of Staffordshire, England. All are incompletely known from the dorsal surface only, and as no characters could be found to separate them, Kjellesvig-Waering's (1986) action seems justified.

EXPLANATION OF PLATE 3

Figs 1–10. *Compsoscorpius elegans* Petrunkevitch, 1949. See Appendix 1 for localities. All specimens Upper Carboniferous (Westphalian B). 1, K14488; femur of walking leg ?4; see Text-figure 4A for explanation; × 26. 2, K14458; femur of walking leg ?3; see Text-figure 4B for explanation; × 32. 3, K14565; patella of walking leg ?3; see Text-figure 4G for explanation; × 26. 4, K14496; tibia of leg 3 or 4; see Text-figure 4D for explanation; × 43. 5, 14484; basitarsus; see Text-figure 4H for explanation; × 32. 6, K14573; basitarsus; see Text-figure 4C for explanation; × 39. 7, K14498; distal end of tibia; see Text-figure 4F for explanation; × 39. 8, K14510; basitarsus; see Text-figure 4E for explanation; × 39. 9, K14480; basitarsus; see Text-figure 4J for explanation; × 39.

Figs 11–16. *Gymnoscorpium mutillidigitus* gen. et sp. nov. See text for localities, all specimens Upper Carboniferous (Westphalian B). 11, K14491; large pedipalp patella, note groups of slit sensilla at distal end; × 26. 12, K14578; paratype, partial pedipalp manus and fixed finger of large individual; × 32. 13, K14497; holotype, pedipalp manus with fixed and free fingers; × 39. 14, K14506; metasomal segment; see Text-figure 4K for explanation; × 32. 15, K14576; metasomal segment; see Text-figure 7L for explanation; × 32. 16, K14575; vesicle and aculeus; see Text-figure 4M for explanation; × 32.



JERAM, *Compsoscorpius*, *Gymmoscorpius*

Dispersed cuticle assemblages containing palaeopisthacanthid-type cuticle have been obtained from several localities in England. Details of these are given above. All of the English palaeopisthacanthid material has been referred to *C. elegans* because only one species can be recognized in the assemblages, and this cannot be reliably distinguished from *C. elegans* which is poorly known. The cuticle material is listed in the Appendix.

Diagnosis. As for genus.

Description. Carapace. An examination of the two specimens with lateral eyes preserved (BMNH I7883 and In15862) confirmed the presence of three major lateral ocelli. It is not possible to tell if minor ocelli are present or not. Unfortunately only a few carapace fragments were recognized in the cuticle assemblages, and none of these has lateral eyes preserved.

Abdomen. Tergites 1–6 lack carinae and are ornamented by evenly distributed small tubercles. Tubercles increase slightly in size posteriorly, and there is a posterior marginal row of bigger tubercles. Setae are sparse (Pl. 1, figs 1–2). The dorsal surface of tergite 7 bears two strong median carinae, delineated by larger tubercles, which converge posteriorly. A pair of weaker lateral carinae are present in large specimens, but are not well developed in juveniles (e.g. K14475). The ventral surface is probably also carinate, but no large specimens are known.

Several partial mesosomal regions were recovered (e.g. Pl. 1, fig. 3; Text-fig. 3A; Pl. 7, fig. 1) which include sternites with stigmata. Stigmata are circular, and slightly closer to the lateral margins than those of *P. schucherti*. Juvenile examples are devoid of ornament, whilst on larger specimens the typical tuberculose ornament is present marginally (Pl. 1, fig. 5). An anterior transverse ridge is present, but it is not produced posteriorly at the lateral margins (cf. tergites). A narrow doublure is present. Four sternites bearing stigmata were probably present in life, although the most complete of the partial specimens (Pl. 7, fig. 1) preserves only three.

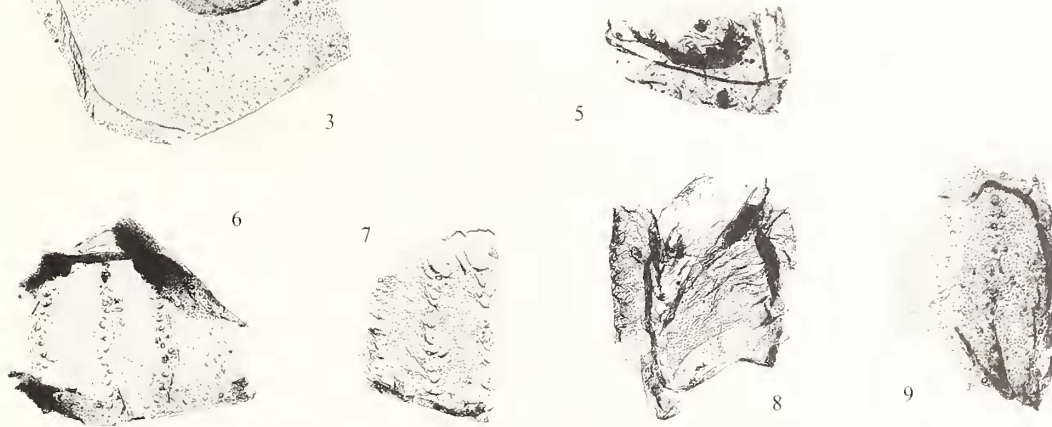
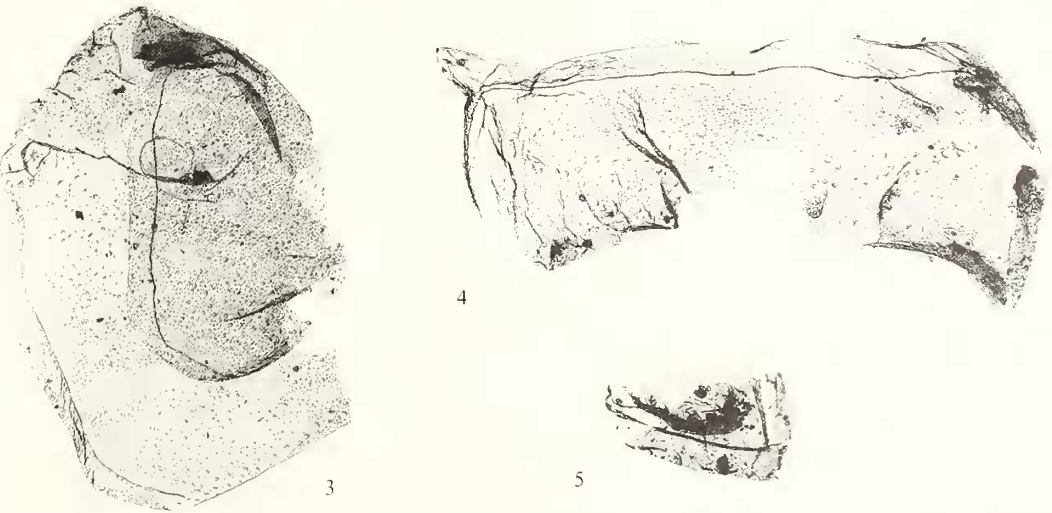
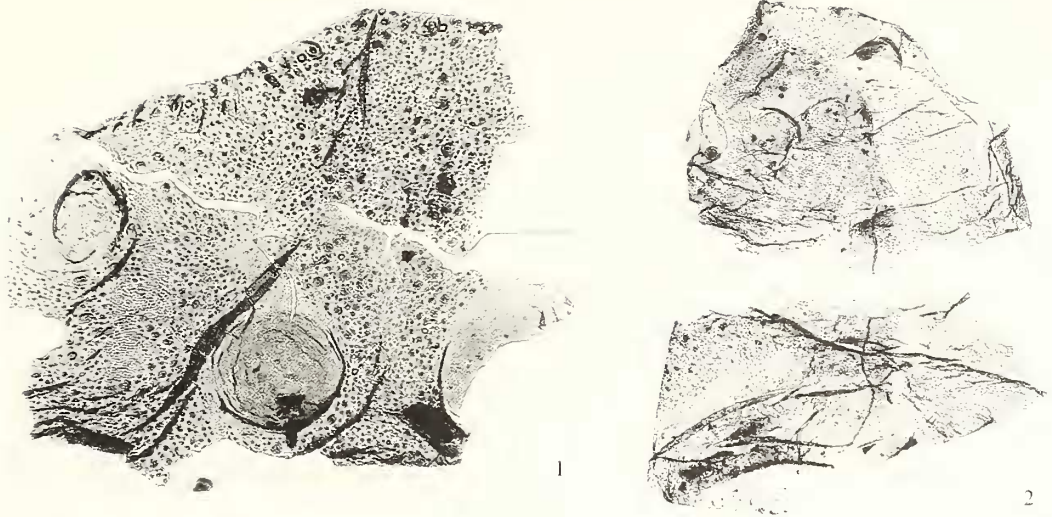
Postabdomen. Metasomal segments are short, but increase slightly in length posteriorly along the tail. The fifth metasomal segment (preanal) is twice as long as the fourth (e.g. BMNH In 15862) and bears much weaker carinae than the others (Pl. 1, fig. 7; Text-fig. 3B). All metasomal segments have an anterior transverse ridge around their entire circumference, and posteriorly a doublure is present. Carinae are delineated by larger tubercles. Dorsal carinae are very prominent (e.g. Pl. 1, figs 8–9; Text-figs 3E, G), but pairs of superior-lateral, inferior lateral and inferior median carinae are also present, making a total of ten carinae per segment.

The vesicle is entirely smooth, except in the largest specimens which have typical palaeopisthacanthid ornament anteriorly. No carinae have been observed. The aculeus is relatively short, and is preserved as very thin pale cuticle. Towards its tip a pair of poison channels can be observed in well preserved specimens (e.g. Pl. 2, fig. 12). The cuticle of the vesicle bears pits approximately 8 μm in diameter and 10 μm deep. They appear as tiny tubercular structures on the inner surface of the fossil cuticle, and at the base of each is a 1 μm diameter pore which presumably connected with a cuticular duct in the inner exocuticle or endocuticle. These have not been observed in other palaeopisthacanthid sclerites, nor in any fossil scorpion cuticle except that of *Gymmoscorpis* gen. nov. (see below).

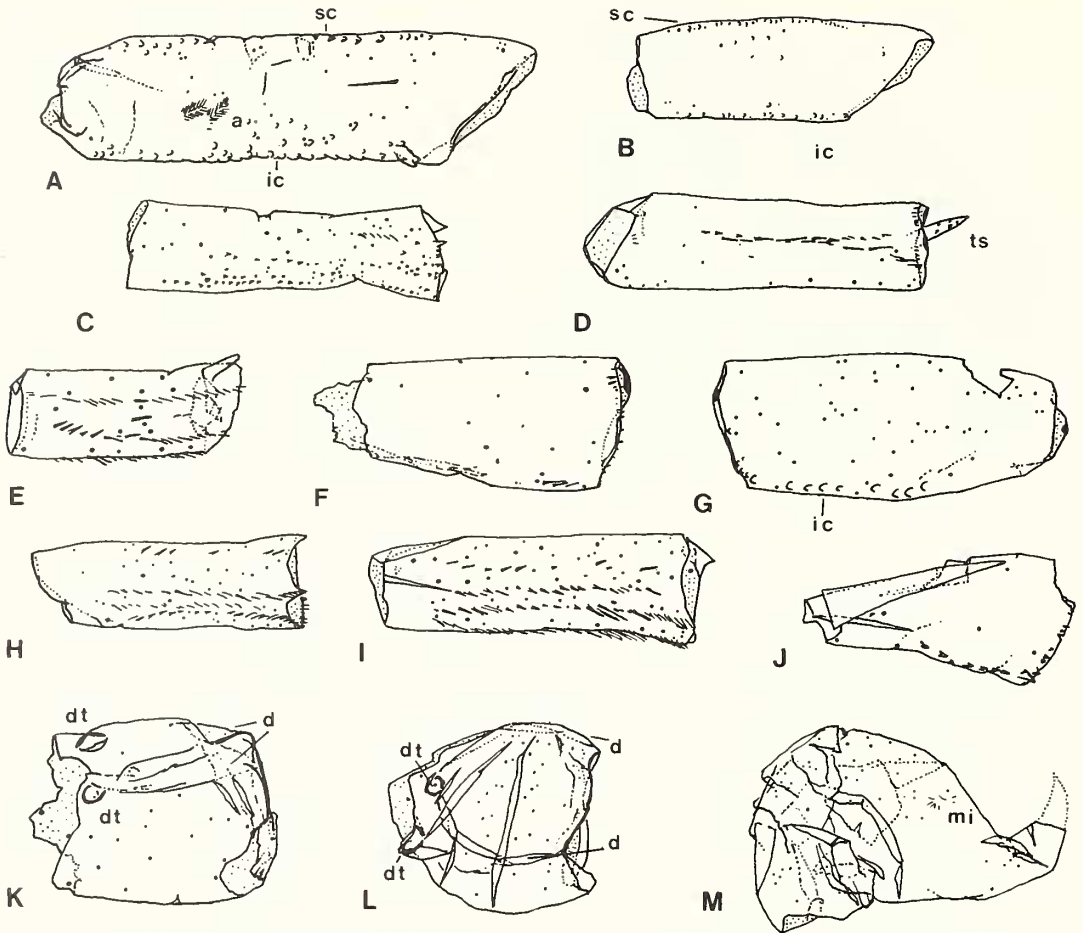
Proosomal appendages. The coxosternal arrangement is not known in its entirety although the apophyses of the first two pairs of walking-leg coxae are visible (but poorly preserved) in BMNH In31261 (Kjellesvig-Waering 1986, text-fig. 107). It is likely that the coxosternal structure is similar to that of *Palaeopisthacanthus*,

EXPLANATION OF PLATE 4

Figs 1–9. *Cryptoscorpis americanus* gen. et sp. nov. All specimens from Lone Star Lake, Kansas; Upper Carboniferous (Stephanian B). 1, K14413; two fragments of an adult carapace; see Text-figure 5A for explanation; $\times 43$. 2, K14081; paratype, two fragments of a folded carapace; see Text-figure 5B for explanation; $\times 26$. 3, K14080; paratype, folded carapace; see Text-figure 5C for explanation; $\times 26$. 4, K14097 (right side) and K14100 (left); dorsal surface of mesosomal tergite 7; see Text-figure 5D for explanation; $\times 26$. 5, K14410; left side of metasomal segment; see Text-figure 5E for explanation; $\times 26$. 6, K14095; ventral surface of metasomal segment; see Text-figure 5F for explanation; $\times 26$. 7, K14411; ventral surface (part) of metasomal segment; see Text-figure 5F for explanation; $\times 26$. 8, K14096; metasomal segment; see Text-figure 5I for explanation, $\times 26$. 9, K14099; right side of metasomal segment; see Text-figure 5G for explanation; $\times 26$.



JERAM, *Cryptoscorpius*

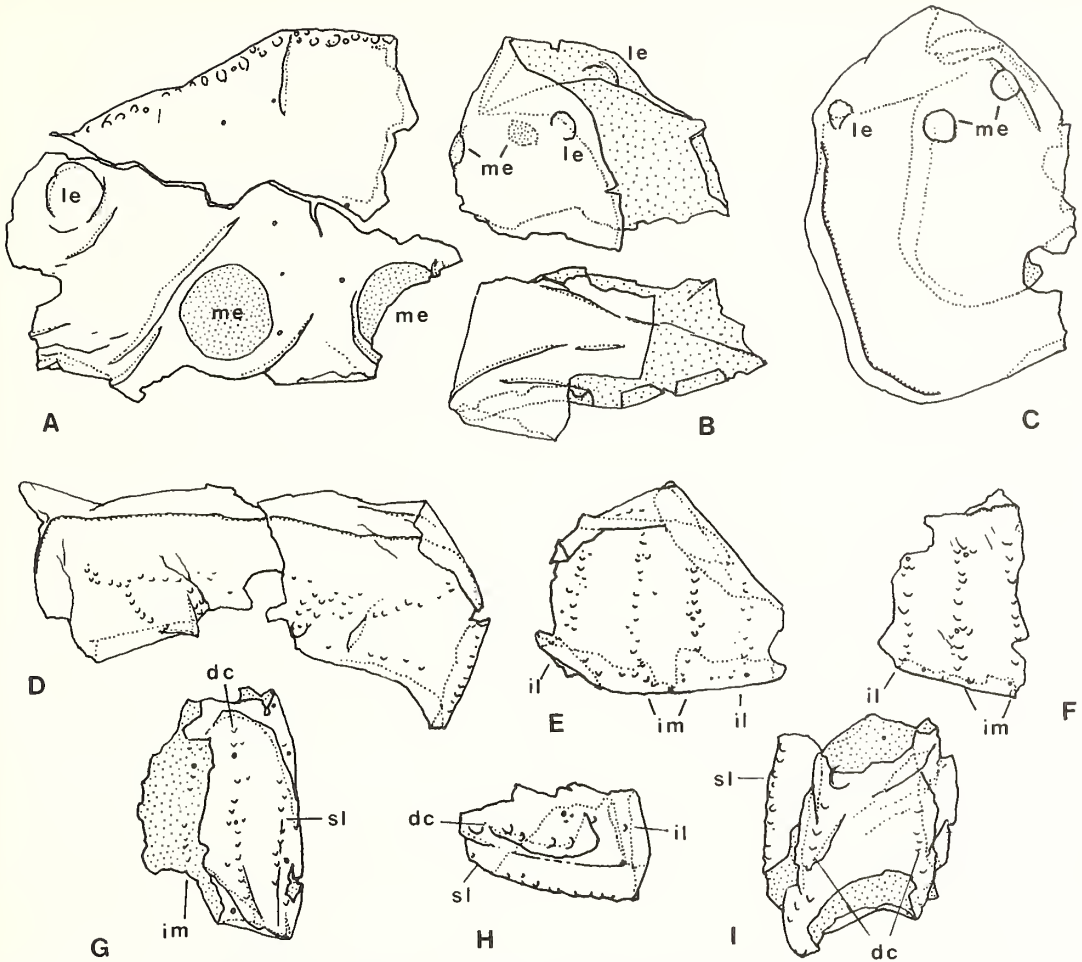


TEXT-FIG. 5. *Compsoscorpis elegans* Petrunkevitch, 1949 (A–J) and *Gymnoscorpis mutillidigitus* gen. et sp. nov. (K–M). Explanatory drawings for specimens illustrated in Plate 3. All specimens from the Westphalian B of England; see Appendix for details of localities and horizons. See Plate 3 for scale. A, K14488; femur of leg ?3, viewed from adaxial side. B, K14458; femur of leg ?2; viewed from adaxial side. C, K14573; basitarsus of posterior leg, viewed from prolatral side. D, K14496; tibia of leg 3 or 4, viewed from inferior side, note tibial spur. E, K14510; basitarsus, distal end crumpled, viewed from inferior side. F, K14498; distal end of tibia, prolatral view. G, K14565; patella of leg ?3, distal end to left, viewed from prolatral side. H, K14484; basitarsus; inferior prolatral view. I, K14480; basitarsus; prolatral view. J, K14526; distal portion of telotarsus with superior part of distal margin missing, lateral view. K, K14506 metasomal segment, anterior margin missing, superior lateral view. L, K14576 metasomal segment, superior view. M, K15475; vesicle and aculeus, the folded tip of the aculeus has been restored to its original position in the drawing. Abbreviations and conventions are given in 'Methods' in the text.

although too little well-preserved material (e.g. Pl. 2, fig. 13) has been recovered to enable a complete reconstruction.

Chelicerae are known only from dispersed cuticle remains. Superiorly the fixed finger bears a large compound tooth consisting of basal and median cusps, a subdistal tooth, and a large distal tooth. Inferior dentition consists of a row of five subequal teeth (Pl. 2, fig. 11; Pl. 6, fig. 6; Text-fig. 4E). The moveable finger has a superior row of five teeth which increase in size distally. The inferior dentition consists of the large distal tooth and an inferior row of approximately twelve small accessory teeth (Pl. 2, fig. 10; Pl. 6, fig. 4).

The pedipalp femur is known from only a few poorly-preserved fragments, but several well-preserved



TEXT-FIG. 6. *Cryptoscorpion americanus* gen. et sp. nov. Explanatory drawings for specimens illustrated in Plate 4. All specimens from Lone Star Lake, Kansas (Stephanian B), see Appendix for details of locality and horizon, and Plate 4 for scale. A, K14413; anterior portion of an adult carapace with both median eyes and left lateral eye group, anterior doublure reaches approximately the level of the tear between the two fragments. B, K14081; laterally compressed carapace, viewed from right side. C, K14080; carapace, left side folded under. D, K14097; dorsal surface of mesosomal tergite 7. E, K14095 ventral surface of metasomal segment with inferior and inferior lateral carinae. F, K14411; fragment of ventral surface of metasomal segment. G, K14099; right side of metasomal segment viewed from dorsal side, dorsal and inferior lateral carinae superimposed. H, K14410; fragment of right side of metasomal segment with strong dorsal carina, posterior end to right, viewed from dorsal side. I, K14096; dorso-ventrally flattened metasomal segment, viewed from dorsal side, part of anterior margin missing. Abbreviations and conventions are given in 'Methods' in the text.

examples of the patella have been recovered (e.g. Pl. 2, figs 6-7). In the original state the pedipalp patella was strongly carinate, each carina being marked by a diffuse row of larger than average tubercles. The precise number of carinae cannot be established in the flattened fossil material, but at least seven were present. Two internal carinae bear particularly large tubercles, each carrying a single setal follicle (Pl. 2, fig. 6). Only two trichobothria are present, and these are identified as eb and et (Text-fig. 4c, f).

The pedipalp manus is approximately half the length of the fixed finger. A row of tubercles marks the dorsal carina, but if other carinae were originally present they cannot be discerned in the fossil specimens. On the external face of the manus there is a large tubercular structure lying just proximally to the eb trichobothrium.

By analogy with similar structures in Recent bothrurids (Maury 1975), it is possible that this is a secondary sexual structure, although it is present in all of the larger manus fragments located so far, which suggests that they were present in both sexes and in sub-adult individuals. Specimens K14490 (Pl. 2, fig. 2; Text-fig. 4A–B), the distal end of a manus, has a trichobothrial distribution similar to that of *Palaeopisthacanthus*. The distribution in proximal regions of the manus is demonstrated by an adult specimen (K14461) although the cuticle is badly crumpled and K14416 was recovered from the same maceration residue as a large free finger (Pl. 2, fig. 5) and may be derived from the same individual. Dentition of the fingers consists of seven slightly oblique, but non-imbricated, primary sub-rows. The basal denticle of each sub-row forms a large tooth and there is a smaller inner accessory denticle on the proximal side of each one. Two large setal follicles are located proximally to the denticle pairs (Pl. 7, fig. 5). Each primary sub-row contains twelve to sixteen denticles.

Walking legs. Femora of walking legs 1–4 are ornamented with superior, inferior, and inferior prolateral carinae. In large specimens these are marked by rows of larger tubercles (Pl. 3, fig. 1; Text-fig. 5A), but the inferior prolateral may not be distinguishable in early instars (Pl. 3, fig. 2). Additional carinae may have been present in life but cannot be detected in the material available. Patellae have a single inferior carina (Pl. 3, fig. 3). In large specimens there is a row of tubercles along the inferior distal margin of the podomere prolaterally. The ornament of fine tubercles is present only on the adaxial surface. Tibiae bear a row of spinules in the distal two-thirds of the inferior surface (Pl. 3, fig. 4; Text-fig. 5D). Distally a second row of spinules is present in large specimens. Small spinules also occur around the prolateral distal margin (Pl. 3, fig. 7; Text-fig. 5F). In one specimen (K14496) from leg 3 or 4, a single tibial spur is present. Basitarsila are ornamented by four rows of fixed spinules. There are two rows located on the inferior surface, a prominent row on the prolateral surface, and a much weaker row on the retrolateral surface (Pl. 3, figs 5, 8–9; Text-fig. 5E, H–I). K14573 has cuticle more heavily ornamented with fine tubercles than other basitarsila of similar size, and the spinules are poorly developed. This may indicate that another species is present, but until further material is found this podomere is included in *C. elegans*, particularly as it exhibits no additional characters of phylogenetic significance. One specimen has been tentatively identified as a telotarsus. This consists of the distal end only of a podomere from a large individual, as indicated by the cuticle thickness and strong ornament, and bears an inferior row of fixed cuticular thorns. A row of tiny spinules is present along the distal margin in the inferior prolateral portion (Pl. 3, fig. 10; Text-fig. 5J). The superior portion of the distal margin is missing, but from the parts preserved it is evident that lateral lobes were not developed.

Discussion. Kjellesvig-Waering (1986, p. 236) diagnosed *Compsoscorpis* simply by reference to its palaeopisthacanthid affinities and the rounded carapace anterior margin. The anterior margin is entire only in the holotype, and its rounded appearance in Kjellesvig-Waering's (1986, text-fig. 105) drawing is illusory, because the carapace is slightly distorted within the nodule.

Genus CRYPTOSCORPIUS gen. nov.

Derivation of name. *Cryptos* (Gr.) – hidden, combined with *skorpis* (Gr.) – a scorpion.

Type species. *Cryptoscorpis americanus* gen. et sp. nov.

EXPLANATION OF PLATE 5

- Fig 1. *Corniops mapesii* gen. et sp. nov. K14082; holotype, pedipalp manus and part of fixed finger; see Text-figure 5A for explanation; Lone Star Lake, Kansas, Upper Carboniferous (Stephanian B); $\times 32$.
 Figs 2–3, 5–10. *Cryptoscorpis americanus* gen. et sp. nov. All specimens from Lone Star Lake, Kansas, Upper Carboniferous (Stephanian B). 2, K14083a; holotype, pedipalp manus and fixed finger; see Text-figure 5B for explanation; $\times 32$. 3, K14404; juvenile basitarsus, proximal end missing; see Text-figure 5C for explanation; $\times 39$. 5, K14085b; partial pedipalp finger; $\times 26$. 6, K14083b; paratype, partial pedipalp manus and fixed finger; see Text figure 6F for explanation; $\times 32$. 7, K14415; femur of walking leg ?3; $\times 26$. 8, K14088; walking leg 4; $\times 26$. 10, K14084a; juvenile trochanter and femur of walking leg ?4; see Text-figure 7E for explanation; $\times 32$.
 Fig. 4. *Palaeopisthacanthus vogelandurdeni* sp. nov. K14086; holotype, distal end of pedipalp manus and fixed finger; see Text-Figure 6D for explanation; $\times 32$.



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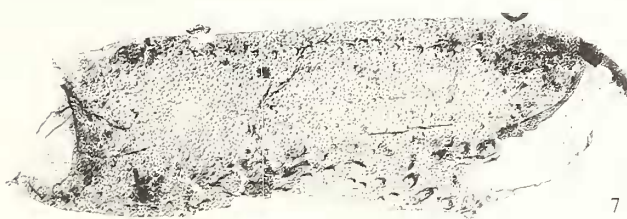
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10

Diagnosis. Palaeopisthacanthid with pedipalp fingers approximately equal in length to manus. Seven primary sub-rows on pedipalp fingers with nine or ten denticles in each.

Cryptoscorpilus americanus sp. nov.

Plate 2, figures 8–9; Pl. 4; Plate 5, figures 2–3, 5–10; Plate 6, figures 1–3; Plate 7, figures 3–4, 7; Text-figures 4D; 6; 7B–C, E–F, H, I; 8A, C–D.

Derivation of name. *americanus*, referring to the geographical province.

Holotype. Pedipalp manus and fixed finger K14083a, from cuticular shale immediately overlying the Lower Williamsburg Coal Member of the Douglas Shale Formation, at Lone Star Lake Spillway, Douglas County, Kansas, USA.

Paratypes. K14083b, incomplete pedipalp manus and fixed finger. K14079, incomplete juvenile scorpion. K14080 and K14081, sub-adult carapaces. All from same locality and horizon as the holotype. Other material is listed in Appendix 1.

Diagnosis. As for genus.

Description. The most complete specimen recovered is a small juvenile in which the prosoma and part of the mesosoma is preserved (Pl. 6, fig. 1; Text-fig. 8A). The specimen is distorted and partly obscured by insoluble opaque organic matter, but nevertheless it reveals several characters which confirm the position of this species in the Palaeopisthacanthidae. In particular, the coxae of walking-legs 3 and 4 both abut the sternum which is sub-pentagonal (in its undistorted state) and slightly longer than broad. The coxal apophyses of walking-legs 1 and 2 (left) have been displaced anteriorly, rotated, and overturned, but are clearly of the palaeopisthacanthid-type, with both apophyses of approximately equal length and breadth. Lateral eye nodes could not be detected on the very thin juvenile cuticle. The first mesosomal sternite, underlying tergite 1 in Text-figure 8A, is very short compared with those of the Recent scorpions, supporting Kjellesvig-Waering's (1986) contention that an anterior sternite underlies the pectines in the holotype of *Palaeopisthacanthus schucherti*, and that four sternites are present in the palaeopisthacanthids. Characters of greater taxonomic use are revealed by the more mature, but fragmentary, material described below.

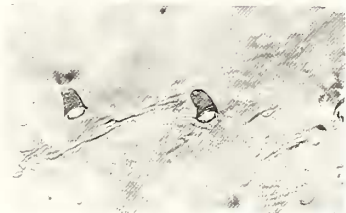
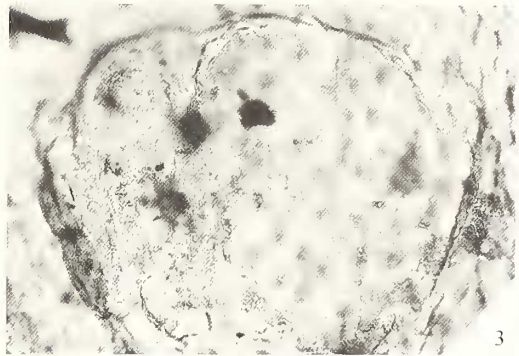
Carapace. Two nearly complete sub-adult carapaces and one partial adult carapace have been recovered, in addition to numerous fragments attributable to this sclerite. The carapace outline is similar to those of *Palaeopisthacanthus* and *Compsoscorpilus*, and there is no evidence of an anterior glossate process. The median eyes are large, and located posteriorly to the lateral eye nodes. Lateral margins are marked by a longitudinal ridge similar to the transverse ridge characteristic of scorpion tergites, and there are rows of larger tubercles along the anterior and posterior carapace margins (Pl. 4, figs 1–3). The lateral eye groups are located on raised

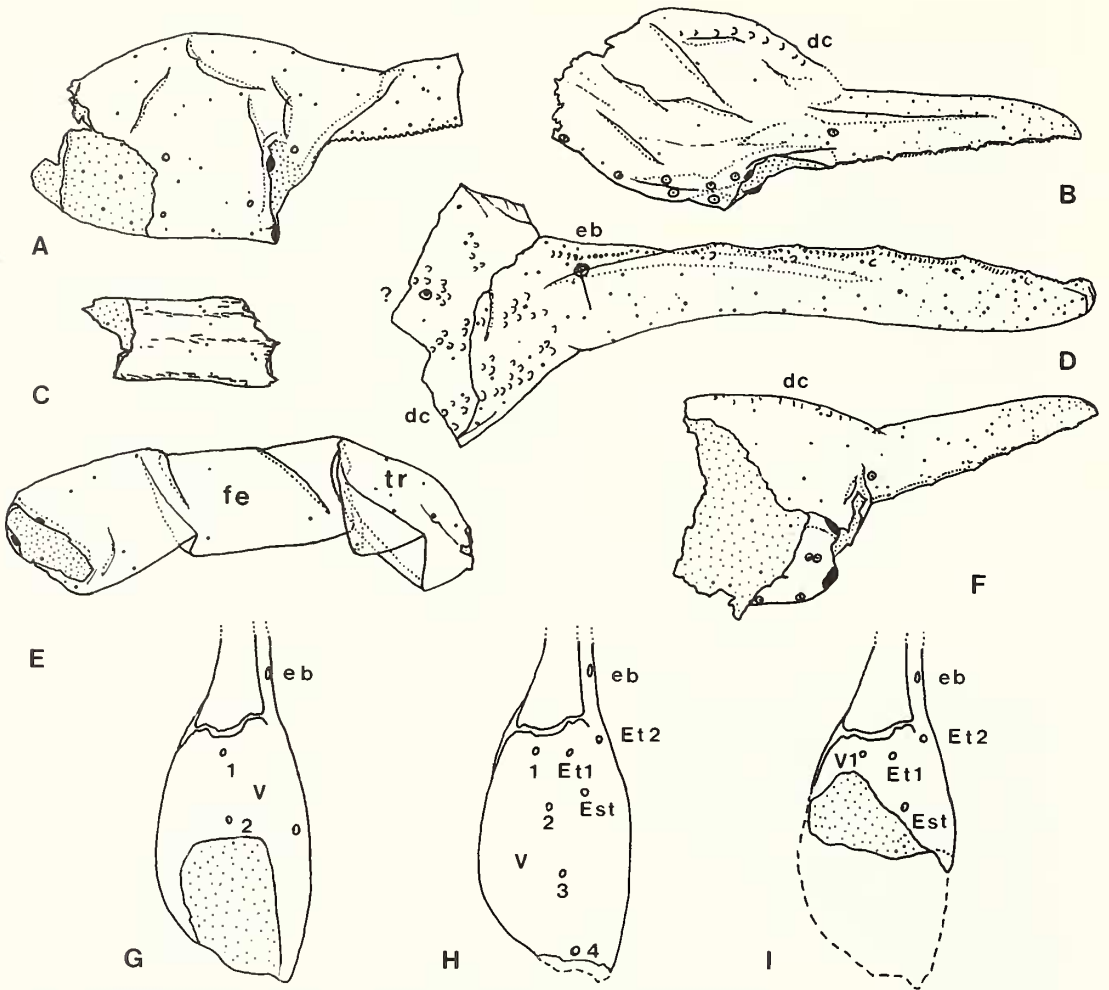
EXPLANATION OF PLATE 6

Figs 1–3. *Cryptoscorpilus americanus* gen. et sp. nov. Lone Star Lake, Kansas; Upper Carboniferous (Stephanian B). 1, K14079; paratype, partial juvenile specimen; see Text-figure 7A for explanation; $\times 32$. 2, K14413; left lateral eye group; see Text-figure 7C for explanation; NDIC photography; $\times 130$. 3, K14081; right lateral eye group; see Text-figure 7D for explanation; NDIC photography; $\times 257$.

Figs 4–7. *Compsoscorpilus elegans* Petrunkevitch, 1949. See Appendix for localities. All specimens Upper Carboniferous (Westphalian B). 4, K14564; detail of cheliceral free finger dentition, viewed from exterior side; NDIC photography; $\times 130$. 5, K14546; detail of cheliceral fixed finger dentition viewed from internal side; NDIC photography; $\times 130$. 6, K14563; inner surface of vesicle cuticle showing two sunken pores; NDIC photography; $\times 257$. 7, K14488; detail of femur cuticle with two probable arachnid tarsila preserved within lumen of podomere; NDIC photography; $\times 130$.

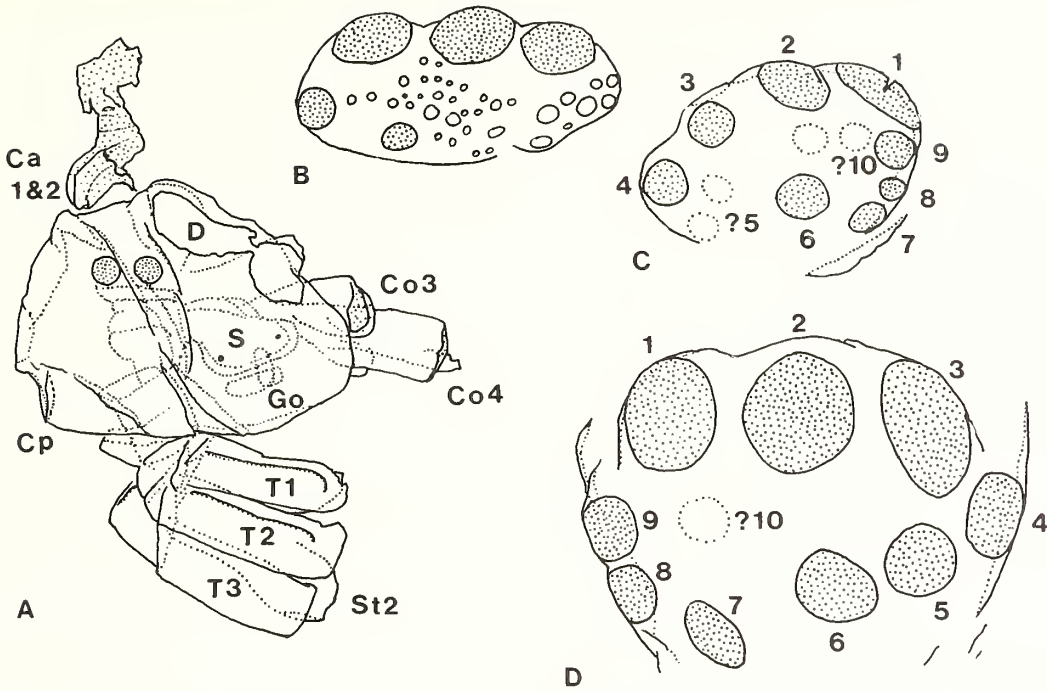
Fig. 8. *Gymnoscorpilus mutillidigitus* gen. et sp. nov. K14575; detail of vesicle cuticle with characteristic form of microseta (top left), and abundant mite setae preserved in lumen of sclerite; Lowther North Opencast Site, Barnsley Seam (Westphalian B); NDIC photography; $\times 257$.





TEXT-FIG. 7. *Corniops mapesii* gen. et sp. nov. (A, G); *Cryptoscorpilus americanus* gen. et sp. nov. (B–C, E–F, H–I); and *Palaeopithacanthus vogelandurdeni* sp. nov. (D). Explanatory drawings for specimens illustrated in Plate 5. All specimens from Lone Star Lake, Kansas (Stephanian B). See Plate 5 for scale. A, K14082; pedipalp manus and part of fixed finger, bothria not designated, see G for explanation; B, K14083a, holotype; pedipalp manus and fixed finger, proximal margin missing. C, K14404; distal end of basitarsus, part of distal margin missing, viewed from inferior side. D, K14086, holotype; distal portion of pedipalp manus and fixed finger, superior surface bottom of drawing, viewed from external side. E, K14084a; trochanter and femur of leg 24; viewed from axial side, distal end on left. F, K14083b; paratype, distal end of pedipalp manus and fixed finger, viewed from internal side. G, reconstruction of trichobothrial distribution in K14082; (see Fig. 7A), viewed from ventral side. H, reconstruction of trichobothrial distribution in K14083a (see Fig. 7B), viewed from ventral side. I, reconstruction of trichobothrial distribution in K14083b; (see Fig. 7F), viewed from ventral side. Abbreviations and conventions are given in the section 'Methods' in the text.

nodes. Ocelli are most evident in the adult specimen (Pl. 6, fig. 2; Text-fig. 8C), but can also be recognized in the other specimens (Pl. 6, fig. 3; Text-fig. 8D). Three major ocelli are present on the external side of the node and up to seven minor ocelli can also be distinguished, although it is not possible in every case to be certain that the features recognized are ocelli rather than tubercles on the eye node. Employing NDIC at high magnification was useful because the cuticle surface of ocelli is much smoother than that of background cuticle,



TEXT-FIG. 8. *Cryptoscorpins americanus* gen. et sp. nov. (A, C–D); *Lychas* sp. (Recent; Buthidae) (B). Explanatory drawings for some specimens illustrated in Plate 6. A, K14079, paratype; partial juvenile specimen viewed from dorsal side, $\times 32$. B, left lateral eye group of Recent buthid scorpion (*Lychas* sp.) showing major and minor ocelli, stippled areas are ocelli, open areas are tubercles on eye node; anterior to right; $\times 50$. C, left lateral eye group of specimen K14413 (see Plate 6, figure 2). Stippled areas are ocelli, broken circles indicate possible ocelli which are numbered anticlockwise from the large anterior ocellus; ocellus no. 5 could not be located with certainty, although there are two patches of cuticle which might represent it; $\times 130$. D, right lateral eye group of specimen K14081 (see Plate 6, figure 3). Drawing conventions as above. Anterior is to left, so numbering of ocelli is clockwise in this specimen; $\times 260$. (In C and D the locations of ocelli were determined by careful use of NDIC microscopy which produces a very small depth of focus, so not all ocelli are clearly visible in the figures on Plate 6). Abbreviations and conventions are given in 'Methods' in the text.

including tubercles, so in certain planes of focus refraction by the ocellar cuticle surface is less than from surrounding cuticle, and the ocelli appear as semi-transparent patches on the cuticle (Pl. 6, fig. 3).

Tergites. Mesosomal tergites 1–6 do not differ in any significant respect from those of other palaeopisthacanthids. However, in large individuals the dorsal surface of tergite 7 bears four strong carinae, each marked by a row of large tubercles. These are present in the posterior half of tergite 7, and anteriorly are linked by a transverse row of tubercles (Pl. 4, fig. 4; Text-fig. 6b). Tergites 1–6 lack carinae.

Sternites. In addition to the incomplete juvenile described above, only a few specimens of sternites have been found, and these are not significantly different from other palaeopisthacanthid sternites.

Metasoma. The caudal segments are similar to those of *Palaeopisthacanthus* and *Compsoscorpins*. Carinae, particularly the dorsal pair, are more prominent, and as in *Compsoscorpins*, an anterior transverse ridge is present around the circumference of each segment (Pl. 4, figs 5–9; Text-figs 6E–I). The vesicle and aculeus are unknown.

Prosomal appendages. The coxosternal arrangement of the species is seen only in the juvenile specimen, K14079, although isolated fragments of coxae, and one complete specimen of coxa 3, have been recovered. Pectines are represented by a fragment associated with two sternites (K14405). This consists of a partial lamina with 14 teeth, although judging by the portion preserved, up to 20 teeth may have originally been present on each comb. Only a small number of well-preserved palaeopisthacanthid podomeres have been recovered from

the Lone Star Lake locality, and so it is not possible to be certain which of these belong to *Cryptoscorpium* or to one of the other taxa in the assemblage. A large (?adult) femur (K14415; Pl. 5, fig. 7) has cuticle with a thickness and intensity of fine tubercles similar to that of the carapace specimen K14413, so it can reasonably be attributed to *Cryptoscorpium*. Almost all of the cuticle ornament is on the adaxial surface of the femur. There are strong inferior, inferior prolateral, and superior carinae, each marked by larger tubercles. The length: breadth ratio of this podomere suggests that it is from walking-leg 3. A second femur (K14084b, Pl. 5, fig. 9) is probably from leg 4. It has thicker, and darker, cuticle than other palaeopisthacanthid podomeres of this size, and in addition to the three carinae present on the specimen cited above, it has a superior prolateral carina. It is approximately the same size as a third specimen, K14084a (Pl. 5, fig. 10; Text-fig. 7E), which appears to lack carinae, and is also unusual in having very little cuticle ornament on the superior surface. K14084a could well be a juvenile of the same species as K14415, but K14084b may be derived from a different species (e.g. *Corniops mapesii* gen. et sp. nov.). However, until more material is available, all podomeres in the assemblage are provisionally attributed to *C. americanus*. A single juvenile patella (Pl. 5, fig. 8) has the rudiments of an inferior carina, and a proximal fragment of the tibia is still articulated with this specimen. Only one example of the basitarsus is known (Pl. 5, fig. 3; Text-fig. 7C). Like *Compsoscorpium*, this has four rows of long spinules; a strong inferior prolateral, two inferior, and a weak inferior retrolateral row. The telotarsus, apotele, and claws are unknown.

ORTHOSTERNI *incertae sedis*

Genus CORNIOPS gen. nov.

Derivation of name. An anagram of 'scorpion'.

Type species. *Corniops mapesii* gen. et sp. nov.

Diagnosis. Dentition of pedipalp finger consisting of single straight file of denticles. No accessory denticles present. Bothria of simple type, without deep cup. Lacking well developed superior carina on pedipalp manus.

Discussion. The cuticle of this genus is of the palaeopisthacanthid-type, but the distinctive pedipalp dentition and bothrial structure exclude it from the Palaeopisthacanthidae. Until further material is recognized the genus can be provisionally regarded as *Orthosterni incertae sedis*, since there are no other derived characters in the only available specimen which are shared with any fossil scorpion.

Corniops mapesii sp. nov.

Plate 5, figure 1; Plate 7, figure 8; Text-figure 7A, G.

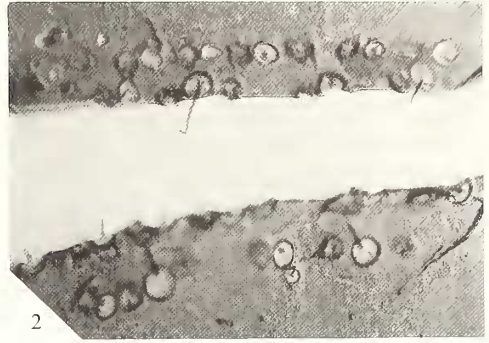
Derivation of name. This species is named for Gene Mapes who recognized the presence of scorpions at the Lone Star Lake locality.

EXPLANATION OF PLATE 7

- Figs 1, 5. *Compsoscorpium elegans* Petrunkevitch, 1949. Swillington Brickpit, Yorkshire; Upper Carboniferous (Westphalian B). 1, K14473; partial juvenile mesosoma with three crumpled sternites, and tergites 5-7; $\times 43$. 5, K14490; detail of pedipalp finger dentition, distal end to right; NDIC photography; $\times 130$.
- Fig. 2. *Gymnoscorpium mutillidigitus* gen. et sp. nov. K14479; holotype, detail of pedipalp dentition, distal end to left; NDIC photography; $\times 257$.
- Figs 3-4, 7. *Cryptoscorpium americanus* gen. et sp. nov. Lone Star Lake, Kansas; Upper Carboniferous (Stephanian B). 3, K14083b; paratype, detail of pedipalp dentition, distal end to left; NDIC photography; $\times 130$. 4, K14083a; holotype, detail of pedipalp dentition, distal end to left; NDIC photography; $\times 130$. 7, K14416; detail of bothrium on fragment of an adult pedipalp ?manus. Note spiralling cristae within cup of bothrium; NDIC photography; $\times 257$.
- Fig. 8. *Corniops mapesii* gen. et sp. nov. K14082; holotype, detail of pedipalp manus viewed from inferior-exterior side; large follicles are probable bothria; dark material is adherent plant cuticle; Lone Star Lake, Kansas; Upper Carboniferous (Stephanian B); NDIC photography; $\times 105$.



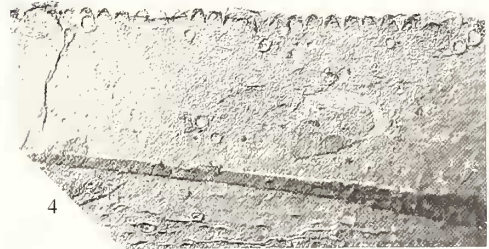
1



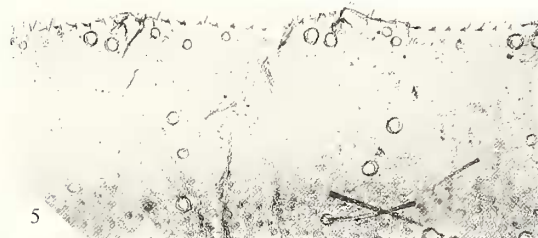
2



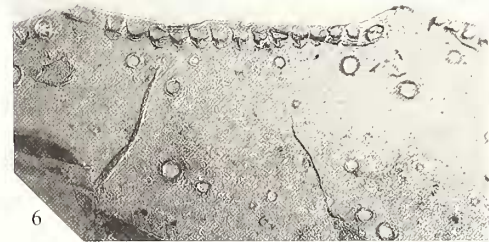
3



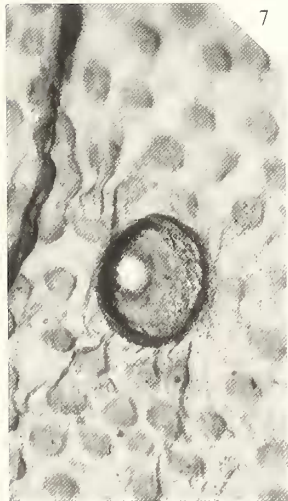
4



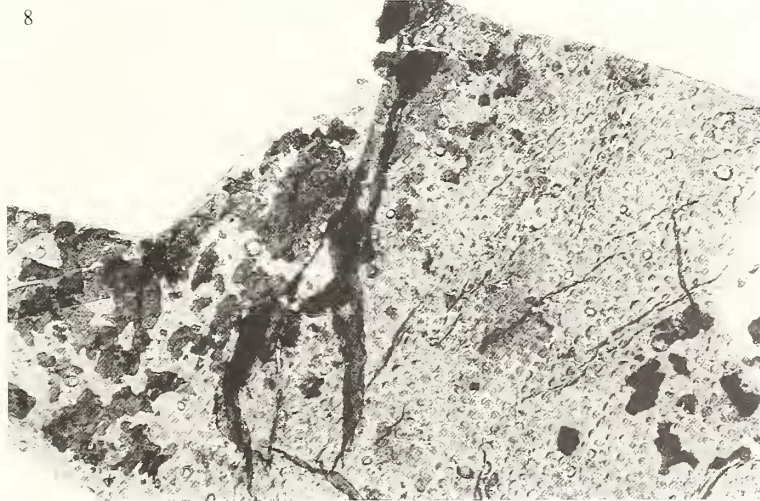
5



6



7



8

Holotype. K14082; the only known specimen, a partial pedipalp manus with proximal portion of the fixed finger. From cuticular shale immediately overlying the Lower Williamsburg Coal, at Lone Star Lake Spillway, Douglas County, Kansas.

Diagnosis. As for genus.

Description. The cuticle is thicker and darker in colour than palaeopisthacanthid pedipalps of a similar size, and the cuticle ornament is bolder and very evenly distributed over the manus. Most setal follicles are small, but a few larger examples are present on the inferior and external surfaces (Pl. 7, fig. 8), and given their positions it is likely that they housed trichobothria. However, their structure is similar to that of normal setal follicles, and no cup-shaped bothria characteristic of palaeopisthacanthids and Recent scorpions are present. Two ventral trichobothria and an eb trichobothrium were probably present. A fourth bothrium lies on the external surface level with V_2 . Unfortunately the proximal part of the manus ventral surface is missing, so it is unknown if any further ventral or basal trichobothria were present originally.

Only a proximal portion of the fixed finger is present, but sufficient is preserved to establish that the dentition consists of a single continuous primary row of denticles, with no accessory denticles present.

NEOSCORPIONINA *incertae sedis*
Genus GYMNOSCORPIUS gen. nov.

Derivation of name. From *gymnos* (Gr.) – naked, and *skorpios* (Gr.) – a scorpion, referring to the cuticle of this genus which lacks macrosetae and is unornamented.

Type species. *Gymnoscopus mutillidigitus* gen. et sp. nov.

Diagnosis. Cuticle lacking macrosetae. Pedipalp fingers equal in length to hand, with poorly defined denticles of palaeostern-type alternating with setal follicles in primary row. Accessory denticles present. Cuticle surface smooth and entirely lacking ornament.

Discussion. This genus cannot be placed in any existing scorpion family, and since the coxosternal configuration, carapace, and sternites, are all unknown its systematic position is problematic. The cuticle characteristics are similar to palaeosterns, as is the form of the pedipalp denticles. Setal characteristics and lack of ornament are unique. Short pedipalp fingers are known in *Garnettius* (the systematic position of which is also problematic) and the Orthosterni. Sunken ducts present in *Gymnoscopus* have only otherwise been observed in palaeopisthacanthids. For the present therefore, *Gymnoscopus* is provisionally assigned to the Neoscorpionina.

Gymnoscopus mutillidigitus sp. nov.

Plate 3, figures 11–16; Plate 6, figure 8; Plate 7, figure 2; Text-figure 5K–M.

Derivation of name. From *mutilatus* (L.) – cut short, combined with *digitus* (L.) – a finger, referring to the short pedipalp fingers of this species.

Holotype. K14479, a complete pedipalp chela with fixed and free fingers, from bed 20F at Swillington Brickpit, near Leeds, Yorkshire.

Paratypes. K14578, an incomplete pedipalp manus and fixed finger from the Barnsley Seam at Lowther North Opencast Mine, Yorkshire. K14491, large pedipalp patella, and K14506, caudal segment, from bed 20F at Swillington Brickpit. K14476, partial femur, from bed 18 at Swillington Brickpit. K14576, caudal segment, and K14575, vesicle, both from same maceration residue, Barnsley Seam, Lowther North Opencast Mine. K14525, cuticle fragment, Wigan Five Foot Coal, Pemberton Opencast Mine, near Wigan, Lancashire.

Diagnosis. As for genus.

Description. Even small fragments of the cuticle are very distinctive. When viewed in transmitted light it has a particularly bright and refractive appearance compared with other fossil scorpion cuticles, and it is smooth, lacking all forms of cuticle surface sculpture or ornament. The openings of cuticular ducts are easily visible, and on the postabdominal segments most take the form of sunken pores (see above). Macrosetae are absent, but sparse microsetae are scattered over the surface and are most abundant on the pedipalp fingers. Prominent clusters of slit sensillae occur near the distal articulations of the pedipalp patella (Pl. 3, fig. 11).

The pedipalp manus is very short, as are the fingers which are approximately the same length as the manus. No trichobothria are present. Pedipalp dentition consists of a single straight primary denticle row in which weakly developed denticles of palaeostern-type alternate with setal follicles. Accessory denticles are present in linear clusters along the fingers (Pl. 3, fig. 13; Pl. 7, fig. 2).

Caudal segments are short and bulbous in shape, lacking lateral and ventral carinae. A pair of dorsal carinae is present, ornamented by a single large tubercle at the anterior end of each carina (Pl. 3, figs 14–15; Text-fig. 5K–L). The vesicle was apparently very bulbous in life, but specimen K14575 is too crushed and complexly folded to reconstruct its shape accurately. The aculeus is short (Pl. 3, fig. 16; Text-fig. 5M). All other parts of this species are unknown.

Remarks. *Gymnoscorpius* is very rare, with only eight specimens recognized from among nearly 12000 Upper Carboniferous scorpion cuticles examined. The largest specimens (e.g. K14578) are derived from individuals with an estimated body length of no more than 30 mm.

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APPENDIX 1

List of material used in study

Belum No.	Brief description	Illustration	Locality
<i>Palaeopisthacanthus schucherti</i>			
K14420	coxa 3, 4 + trochanter	—	7
K14421	postabdominal segment	—	7
K14422	coxal apophyses	—	7
K14423	tergite + sternite	—	7
K14425	tergite	—	7
K14426	pedipalp patella	—	7
K14427	pedipalp femur	—	7
<i>Compsoscorpius elegans</i>			
K14428	pedipalp finger	Pl. 2, fig. 3	1
K14429	tergite	—	5 (18)
K14430	tergite	—	5 (18)
K14432	pedipalp finger	Pl. 2, fig. 5	5 (18)
K14433	postabdominal segment	Pl. 1, fig. 4; Text-fig. 3c	5 (18)
K14434	trochanter	—	5 (18)
K14435	femur	—	5 (18)
K14436	pedipalp manus + fixed finger	—	5 (18)
K14437	tergite	—	5 (18)
K14438	tergite	—	5 (18)
K14440	postabdominal segment	—	5 (18)
K14442	tergite	—	5 (18)
K14444	trochanter	—	5 (18)
K14445	femur	—	5 (18)
K14446	patella	—	5 (18)
K14448	coxa	—	5 (18)
K14449	tergite	—	5 (18)
K14450	tergite	—	5 (18)
K14451	pedipalp manus + fixed finger	—	5 (18)
K14452	trochanter	—	5 (13)
K14454	tergite	—	5 (18)
K14455	tergite	—	5 (18)
K14457	carapace	—	5 (18)
K14458	femur	Pl. 3, fig. 2; Text-fig. 5B	5 (18)
K14460	pedipalp patella	Pl. 2, fig. 6; Text-fig. 4F	5 (18)
K14464	femur	—	5 (18)
K14470	tergite	—	5 (13)
K14471	pedipalp patella	—	5 (13)
K14472	sternite	Pl. 1, fig. 5; Text-fig. 3F	5 (13)

APPENDIX 1 (*cont.*)

Belum No.	Brief description	Illustration	Locality
K14473	partial mesosoma	Pl. 7, fig. 1	5 (13)
K14474	metasomal segment	—	5 (13)
K14475	partial mesosoma	Pl. 1, figs. 1, 3; Text-fig. 3A	5 (13)
K14480	basitarsus	Pl. 3, fig. 9; Text-fig. 5I	5 (20F)
K14481	metasomal segment	Pl. 1, fig. 7; Text-fig. 3B	5 (20F)
K14484	basitarsus	Pl. 3, fig. 5; Text-fig. 5H	5 (20F)
K14485	pedipalp finger	Pl. 2, fig. 1	5 (20F)
K14488	femur	Pl. 3, fig. 1; Pl. 6, fig. 7; Text-fig. 5A	5 (20F)
K14490	pedipalp manus + finger	Pl. 2, fig. 2; Pl. 7, fig. 5; Text-fig. 4A	5 (20F)
K14494	vesicle	—	5 (20F)
K14496	tibia + spur	Pl. 3, fig. 3; Text-fig. 5D	5 (20F)
K14498	tibia	Pl. 3, fig. 7; Text-fig. 5F	5 (20F)
K14499	coxa 2	Pl. 2, fig. 13	5 (20F)
K14500	pedipalp finger	Pl. 2, fig. 4	5 (20F)
K14503	patella	—	5 (20F)
K14504	tergite	Pl. 1, fig. 2	5 (20F)
K14507	femur	—	5 (20F)
K14509	pedipalp ?femur	—	5 (20F)
K14510	basitarsus	Pl. 3, fig. 8; Text-fig. 5E	5 (20F)
K14517	metasomal segment	Pl. 1, fig. 9; Text-fig. 3G	4
K14518	pedipalp	—	4
K14519	femur	—	4
K14521	femur	—	4
K14522	femur	—	4
K14523	?pedipalp trochanter	—	4
K14524	femur	—	4
K14526	telotarsus	Pl. 3, fig. 10; Text-fig. 5J	4
K14527	carapace (fragment)	—	4
K14528	coxal apophyses	—	4
K14529	metasomal segment	—	4
K14530	tergite	—	4
K14531	carapace	—	4
K14532	tergite	—	4
K14533	sternite	Pl. 1, fig. 6; Text-fig. 3D	4
K14535	sternite	—	4
K14537	tergite	—	4
K14539	tergite 7	—	4
K14540	tergite 7	—	4
K14541	sternite	—	4
K14543b	chelicera	—	4
K14545	pedipalp finger	—	4
K14546	chelicera	Pl. 2, fig. 11; Pl. 6, fig. 5; Text-fig. 4E	4
K14547	pedipalp finger	—	4
K14548	femur	—	4
K14549	patella	—	4
K14550	basitarsus	—	4
K14551	vesicle + aculeus	—	5 (20F)
K14552	pedipalp finger	—	6b
K14553	pedipalp manus + finger	—	6b
K14556	pedipalp finger	—	6a
K14557	pedipalp finger	—	6a
K14561	juvenile pedipalp femur	—	6a

APPENDIX 1 (cont.)

Belum No.	Brief description	Illustration	Locality
K14562	pedipalp patella	—	6b
K14563	vesicle + aculeus	Pl. 6, fig. 6	6a
K14564	cheliceral free finger	Pl. 2, fig. 10; Pl. 6, fig. 4	6a
K14565	patella	Pl. 3, fig. 3; Text-fig. 5G	6a
K14566	pedipalp patella	Pl. 2, fig. 7; Text-fig. 4C	6a
K14570	metasomal segment	Pl. 1, fig. 8; Text-fig. 3E	6a
K14571	vesicle + aculeus	Pl. 2, fig. 12	6a
K14573	basitarsus	Pl. 3, fig. 6; Text-fig. 5C	6b
K14579	pedipalp finger + pectine	—	6a
K14580	pedipalp finger	—	6a
K17036	trochanter	—	2
K17036	trochanter	—	2
K17037	?patella	—	2
K17038	femur	—	2
K17039	femur	—	2
K17040	metasomal segment	—	2
K17041	cheliceral free finger	—	2
K17042	cuticle scraps	—	3
<i>Cryptoscorpium americanus</i>			
K14079	paratype partial juvenile	Pl. 6, fig. 1; Text-fig. 8A	8
K14080	paratype carapace	Pl. 4, fig. 3; Text-fig. 6C	8
K14081	paratype carapace	Pl. 4, fig. 2; Pl. 6, fig. 3; Text-figs 6B, 8D	8
K14083a	holotype pedipalp	Pl. 5, fig. 2; Pl. 7, fig. 4; Text-fig. 7B	8
K14083b	paratype pedipalp	Pl. 5, fig. 6; Pl. 7, fig. 3; Text-fig. 7F	8
K14084a	femur + trochanter	Pl. 5, fig. 10; Text-fig. 7E	8
K14084b	femur	Pl. 5, fig. 9	8
K14085a	pedipalp finger	—	8
K14085b	pedipalp finger	Pl. 5, fig. 5	8
K14087	partial mesosoma	—	8
K14088	patella + tibia	Pl. 5, fig. 8	8
K14090	femur	—	8
K14091	pedipalp finger	—	8
K14092	pedipalp finger	—	8
K14093	tergite	—	8
K14094	tergite	—	8
K14095	metasomal segment	Pl. 4, fig. 6; Text-fig. 6E	8
K14096	metasomal segment	Pl. 4, fig. 8; Text-fig. 6I	8
K14097	tergite 7	Pl. 4, fig. 4; Text-fig. 6D	8
K14098	coxa 3	Pl. 2, fig. 9	8
K14099	metasomal segment	Pl. 4, fig. 9; Text-fig. 6G	8
K14100	tergite 7	Pl. 4, fig. 4; Text-fig. 6D	8
K14401	pedipalp ?patella	—	8
K14402	pedipalp femur	Pl. 2, fig. 8; Text-fig. 4D	8
K14403	tergite	—	8
K14404	basitarsus	Pl. 5, fig. 3; Text-fig. 7C	8
K14405	partial mesosoma + pectine	—	8
K14406	tergite	—	8
K14407	tergite	—	8
K14408	tergite	—	8
K14409	tergite	—	8
K14410	metasomal segment	Pl. 4, fig. 5; Text-fig. 6H	8
K14411	metasomal segment	Pl. 4, fig. 7; Text-fig. 6F	8

APPENDIX 1 (*cont.*)

Belum No.	Brief description	Illustration	Locality
K14412	metasomal segment	—	8
K14413	carapace	Pl. 4, fig. 1; Pl. 6, fig. 2; Text-figs 6A, 8C	8
K14414	trochanter	—	8
K14415	femur	Pl. 5, fig. 7	8
K14416	pedipalp patella	Pl. 7, fig. 7	8
K14417	pedipalp ?patella	—	8
K14418	metasomal segment	—	8
K14419	?metasomal segment	—	8
K17048	pedipalp finger	—	8
K17049	tergite	—	8
K17050	metasomal segment	—	8